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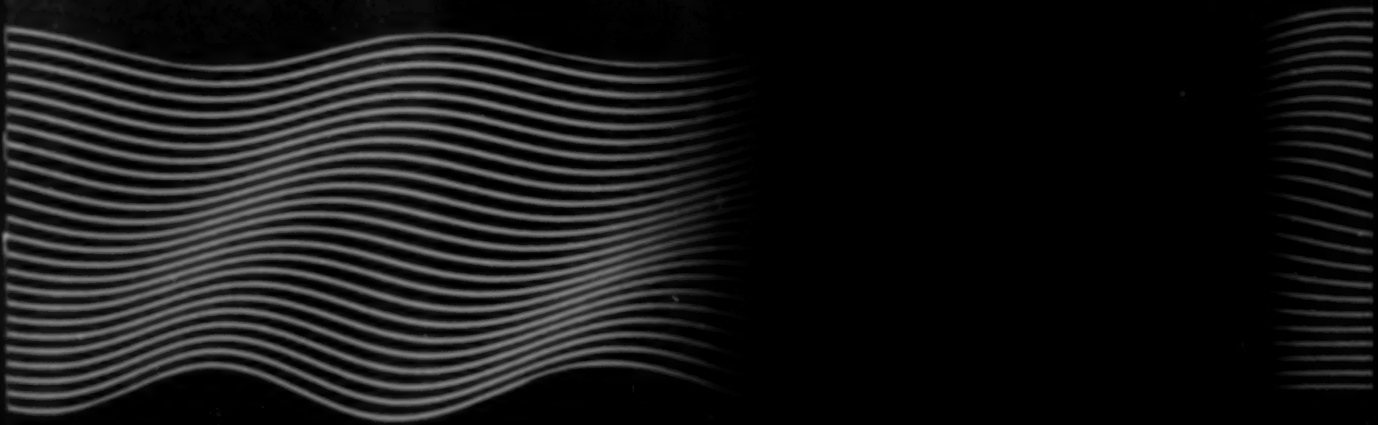

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ANNOUNCEMENT / COMMUNIQUÉ

Dr. Ken Denman and Dr. Trevor Platt honoured at Timothy R. Parsons Award Ceremony, 30 May 2006

Dr. Wendy Watson-Wright, Assistant Deputy Minister for Science of the Department of Fisheries and Oceans (DFO), presented two awards named for Canadian ocean sciences pioneer Dr. Timothy R. Parsons to Dr. Ken Denman and Dr. Trevor Platt, on 30 May 2006, during the 40th Canadian Meteorological and Oceanographic Society Congress in Toronto, Ontario.

Dr. Ken Denman received the award in honour of his career-long contributions on the influence of physical processes on ocean productivity and for pioneering integrated physical–chemical–biological oceanographic research. Dr. Denman is employed at both the Canadian Centre for Climate Modelling and Analysis at the University of Victoria, British Columbia, and the DFO Institute of Ocean Sciences in Sidney, British Columbia.

Dr. Trevor Platt received the award in honour of his outstanding contributions to the fields of biological oceanography and marine ecology, the thermodynamics of the open ocean ecosystem, and an ecosystem approach to fisheries management. Dr. Platt is employed at the DFO Bedford Institute of Oceanography in Dartmouth, Nova Scotia, and is an adjunct faculty member at Dalhousie University in Halifax, Nova Scotia.

For more information on the Parsons medal, visit the website at http://www.dfo-mpo.gc.ca/science/awards/Parsons_ e.htm

MM. Ken Denman et Trevor Platt récipiendaires du prix Timothy R. Parsons, le 30 mai 2006

Le 30 mai 2006, à l'occasion du 40^e congrès de la Société canadienne de météorologie et d'océanographie à Toronto, Ontario, Madame Wendy Watson-Wright (Ph. D.), sous-ministre adjoint au secteur des sciences au ministère des Pêches et des Océans (MPO), a remis à MM. Ken Denman (Ph. D.) et Trevor Platt (Ph. D.) le prix Timothy R. Parsons, nommé pour le pionnier canadien des sciences de la mer.

M. Ken Denman reçoit le prix en reconnaissance de ses travaux tout au long de sa carrière scientifique sur l'influence des processus physiques sur la productivité des océans et parce qu'il est un des premiers à avoir fait l'intégration des aspects physiques, chimiques et biologiques dans la recherche océanographique. M. Denman travaille à la fois au Centre canadien de la modélisation et de l'analyse climatiques à l'Université de Victoria, Colombie-Britannique, et à l'Institut des sciences de l'océan (MPO) à Sidney, Colombie-Britannique.

M. Trevor Platt est récipiendaire du prix en reconnaissance de sa contribution exceptionnelle aux domaines de l'océanographie biologique, de l'écologie marine, de la thermodynamique de l'écosystème de la haute-mer et de l'approche écosystémique dans la gestion des pêches. M. Platt travaille à l'Institut océanographique (MPO) de Bedford à Darmouth, Nouvelle-Écosse, et il est professeur associé à l'Université Dalhousie à Halifax, Nouvelle-Écosse.

Pour plus de renseignements sur la médaille Parsons, visiter le site http://www.dfo-mpo.gc.ca/science/awards/Parsons_f.htm

RAPID COMMUNICATION / COMMUNICATION RAPIDE

A 500-year context for the recent surge in sockeye salmon (*Oncorhynchus nerka*) abundance in the Alagnak River, Alaska

Daniel E. Schindler, Peter R. Leavitt, Susan P. Johnson, and Curtis S. Brock

Abstract: Returns of sockeye salmon (*Oncorhynchus nerka*) to the Alagnak River in Bristol Bay, Alaska, during the last 3 years were unprecedented in the last five decades. Enumerated run sizes averaged about 1 million fish from 1955 to 2002 but surged unexpectedly to average 5.4 million fish in 2003–2005. These huge returns currently pose a challenge to management of Bristol Bay sockeye for several reasons, including that it is unclear whether the recent surge in abundance is a new phenomenon or if it has arisen as part of interdecadal population variability. To answer this question we used changes in lake sedimentary $\delta^{15}N$ coupled with an isotope-mixing model to estimate historical abundances of sockeye salmon populations in this ecosystem. Our analyses show that periods of high salmon abundance have occurred every ~100 years during the last five centuries, interspersed by prolonged periods of substantially lower abundance. We suggest that the recent high returns are an expression of the long-term variability that is characteristic of this stock and will be a relatively transient phenomenon.

Résumé : Au cours des 3 dernières années, les retours de saumons rouges (*Oncorhynchus nerka*) de la rivière Alagnak dans la baie de Bristol, Alaska, ont été sans précédent pendant les cinq décennies antérieures. Les tailles moyennes des montaisons de 1955–2002 ont été estimées à 1 million de poissons; de façon inattendue en 2003–2005, elles ont augmenté à une moyenne de 5,4 millions de poissons. Ces retours massifs posent actuellement des problèmes pour la gestion des saumons rouges de la baie de Bristol pour plusieurs raisons, en particulier parce qu'il n'est pas clair si cette augmentation récente de l'abondance est un phénomène nouveau ou si elle fait partie de la variabilité de la population au cours des décennies. Afin de répondre à la question, nous utilisons les changements dans le $\delta^{15}N$ des sédiments conjointement à un modèle de mélange des isotopes afin d'estimer les abondances passées des populations de saumons rouges dans cet écosystème. Nos analyses révèlent qu'il s'est produit des périodes de fortes densités de saumons environ tous les 100 ans au cours des cinq derniers siècles avec de longs intervalles d'abondances substantiellement plus basses. Nous croyons que les retours importants actuels sont l'expression de la variabilité à long terme de ce stock et qu'ils représentent un phénomène relativement transitoire.

[Traduit par la Rédaction]

Introduction

Fisheries management often assumes that fish abundance can be quantified as a stationary parameter (constant mean and variance) that is characteristic of a particular ecosystem. In addition to the convenience of assuming stationarity, stock assessment data are often too poor in quality or too short in duration to properly assess whether abundance varies over long time periods (Walters 1987). Management strategies assuming stationarity can result in suboptimal harvest if the underlying abundance is changing (Walters and Parma 1996) and can increase the risk of overharvesting the population under certain management strategies (i.e., those that attempt to maintain high harvested biomass). Although environmentally driven changes in the abundance of fish stocks is a critical component of sustainable fisheries, management rarely considers how this aspect of ecosystems varies over long time scales.

Sockeye salmon (*Oncorhynchus nerka*) populations in Bristol Bay, southwest Alaska (Fig. 1*a*), have been characterized

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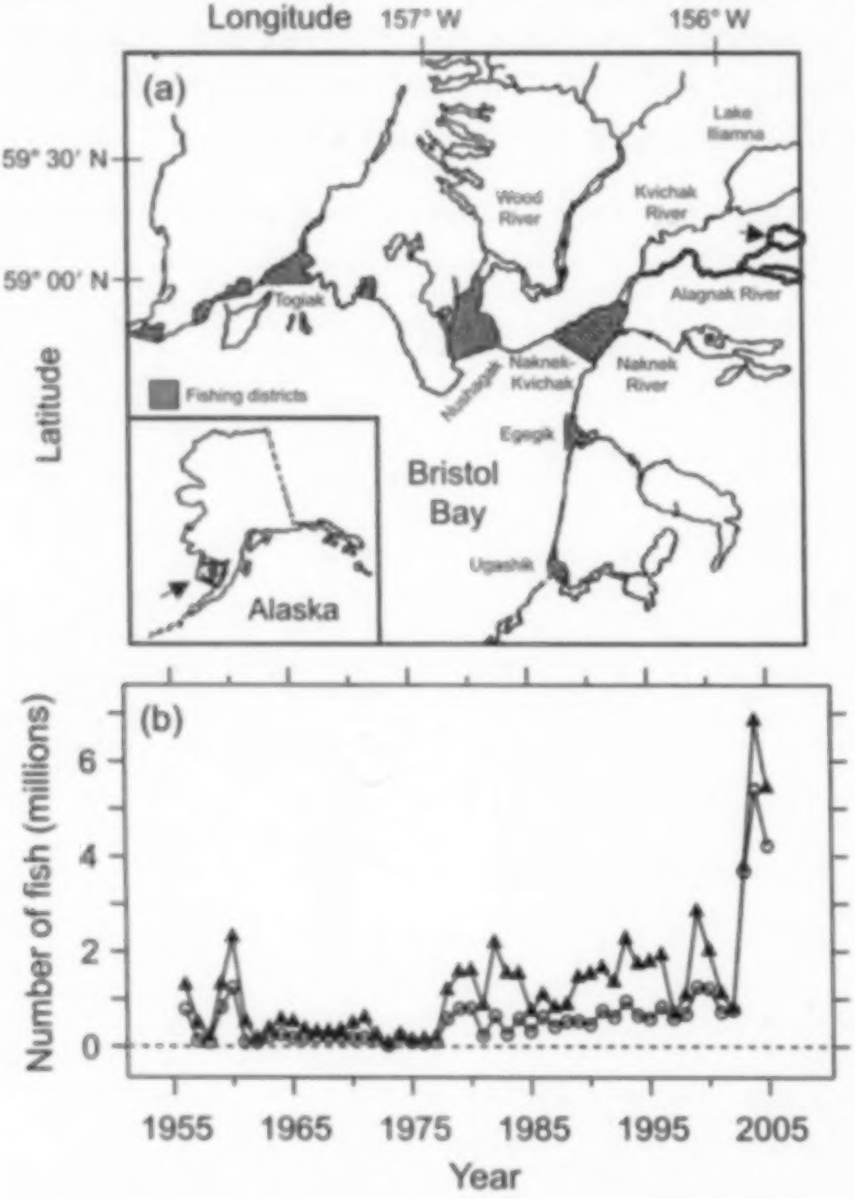
Fig. 1. (*a*) Map of Bristol Bay, Alaska, showing the major fishing districts for sockeye salmon (*Oncorhynchus nerka*; hatched regions) and the location of the Alagnak River. The arrow in the large panel points to Kukaklek Lake, the site where the lake sediment core was extracted to reconstruct sockeye salmon populations in the Alagnak system. (*b*) Total run and escapement dynamics of sockeye salmon in the Alagnak River from 1955 to 2005. Data are from the Alaska Department of Fish and Game (Clark 2005).



by long-term variation in abundance that, in general, has correlated with the major phases of the Pacific Decadal Oscillation (Mantua et al. 1997). However, when total sockeye abundance is divided into the major river districts that provide spawning and nursery habitats for the stock complex, the performance of individual stock components has differed during the last century (Hilborn et al. 2003; Peterman et al. 2003), with some populations (e.g., Egegik River) having had distinct periods of high abundance, interspersed by periods of distinctly lower abundance. Others (e.g., Wood River) have been building slowly throughout most of the last century. In contrast, the Kvichak River stock, which was the single largest sockeye population in the world for most of the last century, has recently shown a substantial decline in abundance to the point at which the fisheries on this river are now severely restricted in an attempt to conserve this stock component (Fair 2003).

One of the biggest surprises in the dynamics of Bristol Bay sockeye has been the substantial and abrupt increase in the Alagnak River sockeye population in recent years (Clark 2005). Enumerated run sizes averaged ~1 million fish during 1955–2002 but surged to an average of 5.4 million fish in 2003–2005 (Fig. 1*b*). Because the fish from this stock are caught in a mixed-stock fishery, i.e., combined with those from the Naknek and Kvichak rivers (Fig. 1*a*), it is unclear whether the recent huge returns to the Alagnak River are the result of reduced fishing pressure to conserve the Kvichak stock or whether the productivity of the freshwater and marine habitats used by Alagnak River fish has increased abruptly. This uncertainty has prevented development of a rational long-term management strategy for the Alagnak stock.

We used paleolimnology to reconstruct the long-term changes in the abundance of sockeye salmon returning to the Alagnak River system to put the recent population changes into a five-century historical context. Because death of salmon after spawning releases nitrogen enriched in the ^{15}N isotope in proportion to the number of fish returning to a system, and because this isotope signature is preserved in lake sediments (Finney et al. 2000), estimates of changes in sedimentary N isotope ratios can be used to reconstruct historical population dynamics of sockeye salmon (Schindler et al. 2005). Our reconstructions show that the abundance of the Alagnak River sockeye stock has varied considerably at centennial time scales over the last five centuries, and the recent stock buildup coincides with the periodicity of past production peaks.

Materials and methods

Site description

The Alagnak River, a tributary of the Kvichak River flowing into Bristol Bay, Alaska (Fig. 1*a*), is a major spawning and nursery system for sockeye salmon. Most of the sockeye spawning occurs in the tributaries flowing into two large lakes (Kukaklek and Nonvianuk), which are also used as nursery grounds for juvenile sockeye before their migration to the ocean (Clark 2005). Kukaklek Lake receives about 70% of the spawning run (Clark 2005); therefore, we used this site for paleolimnological reconstructions of past sockeye runs in the Alagnak system. We used Tazimina Lake in the upper Kvichak drainage and Grant Lake from the upper Wood River drainage as reference sites to establish background variability in sediment characteristics independent of sockeye populations. These lakes have substantial waterfalls on their outflows that render them inaccessible to anadromous fishes.

One sediment core was collected from a depth of 35 m in Kukaklek Lake and another from a depth of 30 m in Tazimina Lake by float plane in September 2004 using a Glew gravity corer (John Glew, Paleolimnological Environment Assessment and Research Laboratory, Queens University, Kingston, Ontario). Previous analyses of the spatial heterogeneity of the δ^{15}N in surface sediments of similar Bristol Bay sockeye nursery lakes demonstrated that a single, representative core was adequate to reconstruct historical variation in sedimentary δ^{15}N because spatial variation in δ^{15}N was low within any single lake (coefficient of variation ~16%; Brock et al. 2006). Grant Lake was previously cored in August 2003 as described in Schindler et al. (2005). All cores were separated into 1.7 mm slices in the field and frozen immediately at –10 °C in the dark. This sectioning interval translated into data intervals that averaged 3.4 years (standard deviation (SD) = 1.7 years) and, as a result of sediment compaction, were of slightly shorter duration in the upper sections of the core than in the deeper sections. Within 3 months, core samples were thawed, freeze-dried to constant mass, and analyzed for isotope content.

Sediment chronology

Sediment ages were estimated from down-core declines in ^{210}Pb activity using the CRS (constant rate of supply) model of Binford (1990). Samples for analysis of ^{210}Pb activities were dried to constant mass at 50 °C, homogenized, and analyzed for ^{210}Pb using alpha-spectrometric analysis by Flett Industries (Winnipeg, Manitoba, Canada). All counting times were 8.3 h. The standard deviations of estimated sediment ages from the CRS model increased down-core to about ±17 years by 1830 (i.e., coefficient of variation ~10%). Ages of older strata were extrapolated from the equilibrium sedimentation rate estimated from the CRS model (Binford 1990).

Stable nitrogen isotopic composition

Stable nitrogen isotope distributions were determined by continuous-flow isotope ratio mass spectrometry using a Delta XL isotope ratio mass spectrometer with an automated Carlo Erba elemental analyzer inlet device. Analytical precision of this instrument was ±0.08‰ for δ^{15}N, well below the variation in δ^{15}N observed among and within lakes attributable to variation in salmon abundance. Stable isotope ratios were expressed as $\delta^{15}\mathrm{N} = (R_{\mathrm{sample}}/R_{\mathrm{standard}} - 1) \times 1000$, where R_{sample} represents ^{15}N/^{14}N in the sample, and R_{standard} is the corresponding isotope ratio from the atmospheric nitrogen.

Isotopic mixing model and salmon run sizes

We used a two-member mixing model (Schindler et al. 2005) to translate changes in sedimentary δ^{15}N into historical variation in escapement (E_t) within the Alagnak River system. We assumed that sockeye returns to the tributaries of Kukaklek Lake were a reasonable indicator of sockeye abundance throughout the entire Alagnak system (Clark 2005).

The mixing model is expressed as

$$E_t = N_{\mathrm{ws}} R_t + e_t$$

where

$$R_t = \left(\frac{\delta^{15}\mathrm{N}_{\mathrm{sed},t} - \delta^{15}\mathrm{N}_{\mathrm{ws},t}}{\delta^{15}\mathrm{N}_{\mathrm{salm}} - \delta^{15}\mathrm{N}_{\mathrm{sed},t}} \right)$$

N_{ws} is the amount of N loaded from the watershed to the lake expressed in the same units as escapement, $\delta^{15}\mathrm{N}_{\mathrm{sed},t}$ is the δ^{15}N of the sediments from Kukaklek Lake representing a mixture of nitrogen loaded from salmon and from the watershed at time *t*, $\delta^{15}\mathrm{N}_{\mathrm{ws},t}$ is the δ^{15}N from watershed sources at time t, $\delta^{15}N_{salm}$ is the $\delta^{15}N$ of sockeye salmon tissue, and e_t are random normal errors with mean equal to zero. Thus, N_{ws} is the only unknown term and can be estimated by regressing E_t against R_t for the period when E_t was enumerated directly.

We used the enumerated escapement (E_t) to the Alagnak system for the period 1955–2002 (Clark 2005) and the corresponding changes in R_t to estimate N_{ws}. Escapement to the Alagnak River is monitored by the Alaska Department of Fish and Game using a combination of tower-count and aerial surveys. Tower counts were performed from 1955 to 1976 and from 2001 to present by enumerating fish migration upstream on the main stem of the river for 10 min on each bank for every hour throughout the spawning run (Clark 2005). Aerial surveys during 1977–2000 were expanded to total escapement numbers based on the relationship between escapement based on tower counts and escapement based on aerial surveys derived for years when both methods were used (n = 9 years; Clark 2005). Because the values of R_t are obtained from sediment samples that include more than 1 year of time, and because sediment mixing causes some blurring of the salmon-derived nitrogen signature in the sedimentary record, we smoothed the enumerated escapement data with a 5-year running mean before estimating N_{ws}. Values of E_t from the smoothed series were selected to match the average age of each of the 25 sediment samples from Kukaklek Lake between 1955 and 2003.

We ran four different model scenarios to account for variation in $\delta^{15}N_{ws}$ in the calculation of R_t. Two scenarios simply used the average value for each of the two reference systems and assumed that this parameter was constant. We also ran two additional scenarios that accounted for the observed changes in $\delta^{15}N$ in the sediment cores from the reference lakes. For these latter scenarios, the $\delta^{15}N$ values from each of the reference systems were linearly interpolated to establish values for $\delta^{15}N_{ws,t}$ that matched the dates for each sample from the Kukaklek core. We assumed that $\delta^{15}N_{salm}$ was constant through time and equal to 11.2‰ (Schindler et al. 2005).

We used a Morlet wavelet transform (Torrence and Compo 1998) to evaluate periodicity in the historical time series of sockeye abundance in the Alagnak River. To accomplish this we combined the enumerated abundances (sum of catch and escapement, smoothed with a 5-year running mean) from 1955 to the present with the historical abundances from 1507 to 1955 determined from our paleo-reconstructions. This combined time series was then interpolated to obtain abundance values corresponding to a regular 4-year interval (i.e., approximate average time interval represented by the sediment core analyses). The power spectrum was calculated according to Torrence and Compo (1998; software available at http://paos.colorado.edu/research/wavelets/).

Results and discussion

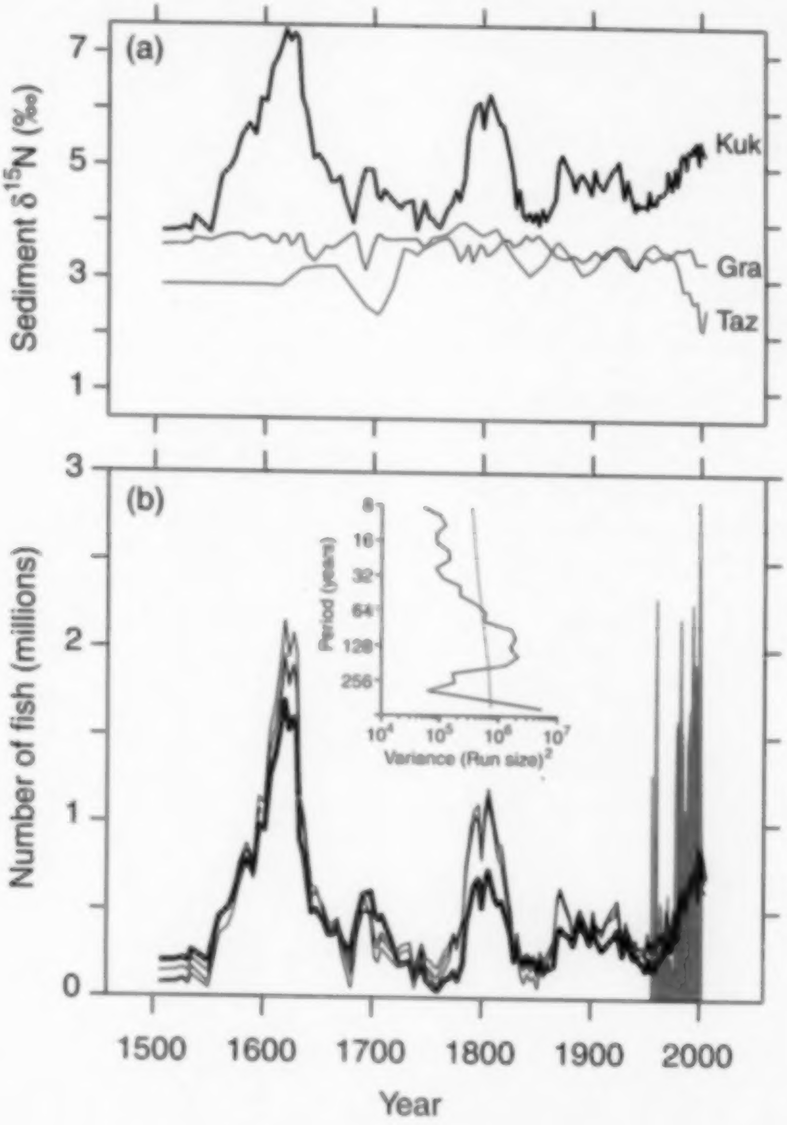
Sediments from the sockeye salmon nursery lake (Kukaklek) were more enriched in ^{15}N than the sediments from either reference lake (Fig. 2*a*). The $\delta^{15}N$ from Kukaklek Lake averaged 4.3‰ (SD = 0.6‰) compared with 2.8‰ (SD = 0.5‰) and 3.1‰ (SD = 0.2‰) for Tazimina and Grant lakes, respectively. This enrichment of ^{15}N is indicative of the deposition and retention of salmon-derived nutrients (SDN) in the sediments of Kukaklek Lake. In addition, the substantial increases in escapement to the Alagnak River from 1955 to the present provided a convenient contrast in SDN deposition to test whether these escapement increases were faithfully archived in the sedimentary record. Indeed, the upswing in escapement during this time period was paralleled by a substantial increase in the $\delta^{15}N$ in the recent sedimentary record of Kukaklek Lake (Fig. 2*a*).

The best model fit to the smoothed escapement data was obtained using the observed dynamics in $\delta^{15}N_{ws}$ from the Tazimina Lake reference core. This yielded a value of 1.66 × 10^6 sockeye equivalents for N_{ws}, which produced model predictions in good agreement with historical escapements for the last five decades ($r^2 = 0.69$, $n = 25$). This value of N_{ws} was then applied throughout the 500-year reconstruction of E_t. Values of N_{ws} fit from the other three model scenarios were somewhat higher (mean 2.28 × 10^6, SD = 0.19 × 10^6) and did not produce fits to the data that were as good as the Tazimina scenario (r^2 range 0.46–0.6) but were used to produce historical model reconstructions for comparison purposes.

Our reconstructions of historical population dynamics of sockeye salmon in the Alagnak River suggest that this stock has been highly variable and distinctly periodic during the last five centuries (Fig. 2*b*). There were three major peaks of enhanced abundance: the first around 1600, the second around 1800, and the last around 2000. These major peaks were interspersed by two smaller abundance peaks centered about 1700 and 1900. Each of the major abundance peaks lasted about 20–50 years and was interspersed by several decades of substantially reduced abundance. A wavelet analysis (Torrence and Compo 1998) performed on the combined time series shown in Fig. 2*b* demonstrates that sockeye abundances have varied with a centennial oscillation during the last five centuries (Fig. 2*b*, inset). Thus, the recent buildup of the population, culminating in the record returns observed in the last 3 years, has occurred at about the expected time based on the periodicity in the abundances over the last five centuries. In light of this pattern, the buildup of the Alagnak stock since 1955 (Figs. 1*b*, 2*b*) is revealed as part of a long-term cycle, the cause of which is presently unknown. If the historical cyclical nature of the stock still applies to the current dynamics, our analyses suggest that returns observed in the last few years occurred near the expected production peak and that we should begin to see abundance taper off again in the near future.

The increase in abundance of Alagnak sockeye since the mid-1970s is generally consistent with both the increased abundances in several other Bristol Bay stocks during this time period (Hilborn et al. 2003; Peterman et al. 2003) and the centennial-scale periodicity observed in the Kukaklek Lake sediment record. Temporal changes in sockeye abundance from the Alagnak system also show some of the same general patterns of interdecadal variation observed in two other Bristol Bay salmon stocks over the last three centuries (Finney et al. 2000). However, the extent of the recent surge in Alagnak sockeye abundance compared with other Bristol Bay stocks and the fact that some Bristol Bay stocks have

Fig. 2. (*a*) Chronologies of sedimentary $\delta^{15}N$ from Kukaklek Lake (Kuk) and the two reference lakes with natural blockages to sockeye (*Oncorhynchus nerka*): Grant Lake (Gra) and Tazimina Lake (Taz). (*b*) Reconstructed time series of sockeye salmon abundance in the Alagnak River from the four different baseline scenarios discussed in Materials and methods. The heaviest line is from the scenario with the best fit to the data (i.e., using Tazimina Lake as the reference). The shaded region represents the total enumerated annual run size to the Alagnak River from 1955 to 2002 (Clark 2005). Values for 2003–2005 were omitted because they were off scale. Note that the total enumerated run size greatly exceeds the reconstructed escapement since 1955, because fish that were intercepted by fisheries (average, 47% of run; range, 3%–83%) are included in the enumerated run size but are not archived in the lake sediments. Also note that fishery catch data are not available before 1955 but that commercial fisheries have been in operation since the 1890s. Inset shows the global wavelet power spectrum for the combined time series relative to the 5% significance boundary (dotted vertical line).



shown declines in abundance during this same time period emphasize the heterogeneity of population responses to changing environmental conditions within the Bristol Bay stock complex (Hilborn et al. 2003; Peterman et al. 2003). Thus, the recent surge in Alagnak sockeye abundance should be viewed as one expression of the biocomplexity within Bristol Bay sockeye salmon.

Inspection of the last five decades of Alagnak sockeye abundance within the context of the last five centuries of historical dynamics suggests that this stock was more abundant since the late 1970s than during most of the last 500 years. However, total run size during the last 20 years has been about two million fish (Clark 2005), which is very comparable with the peak densities that occurred for about two decades in the early 1600s (Fig. 2*b*). Taken together, our results suggest that the record returns to the Alagnak River observed recently were not simply a result of the conservation measures recently placed on Kvichak River fish. Instead, the recent surge in abundance of Alagnak River sockeye appears to be an expression of their long-term population dynamics and is likely to be a transient phenomenon.

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RAPID COMMUNICATION / COMMUNICATION RAPIDE

When do marine reserves increase fishery yield?

Deborah R. Hart

Abstract: An age-structured model is developed for analyzing the effects of marine reserves and other long-term closures on fishery yield, assuming larvae are well-mixed and that exchange of adults between the open and closed areas is negligible. A number of analytic results are derived, including a formula for the gradient of yield with respect to fishing mortality and closure fraction. Increasing the closure fraction at equilibrium spawning stock biomass (SSB), B, will increase yield if and only if $s'(B) > 1/b_0(0)$, where $s'(B)$ is the slope of the stock–recruitment curve at B and $b_0(0)$ is SSB per recruit at zero fishing mortality. Conditions for the level of closure required to prevent stock collapse are also derived. Applications of the theory to canary rockfish (*Sebastes pinniger*) and Georges Bank sea scallop (*Placopecten magellanicus*) illustrate that long-term closures increase yield only at low SSB associated with fishing mortalities greater than F_{MSY} and with low closure fractions. The theory presented here gives simple analytic and graphical techniques for predicting the effects of long-term closures on yield and stock persistence.

Résumé : Un nouveau modèle structuré d'après l'âge permet d'analyser les effets des réserves marines et des autres fermetures de longue durée de la récolte sur le rendement de la pêche, si l'on présume que les larves sont bien réparties et que les échanges d'adultes entre les zones ouvertes et fermées sont négligeables. Il en dérive plusieurs résultats analytiques, dont une formule pour déterminer le gradient du rendement en fonction de la mortalité due à la pêche et la fraction représentée par les zones fermées. L'accroissement de la proportion des zones fermées lorsque la biomasse du stock reproducteur (SSB) est à l'équilibre B va faire augmenter le rendement seulement si $s'(B) > 1/b_0(0)$, où $s'(B)$ est la pente de la courbe stock–recrutement au point B et $b_0(0)$ est la SSB par recrue lorsque la mortalité due à la pêche est nulle. On peut aussi obtenir les conditions du niveau de fermeture nécessaire pour prévenir l'effondrement du stock. Des exemples utilisant le sébaste canari (*Sebastes pinniger*) et le pétoncle marin (*Placopecten magellanicus*) du banc Georges montrent que les fermetures de longue durée de la pêche augmentent le rendement seulement lorsque des SSB basses sont associées à des mortalités dues à la pêche supérieures à F_{MSY} et que les fractions des zones fermées sont petites. La théorie présentée ici fournit des techniques analytiques et graphiques simples pour prédire les effets de fermetures de longue durée sur le rendement et la persistance des stocks.

[Traduit par la Rédaction]

Introduction

There has been enormous interest in recent years in long-term fishery closures, often termed "marine reserves", as a management tool. Although there is little question that such closures can be part of a precautionary approach to fisheries management, their effect on fishery yields is more controversial. Although increases in biomass within closures and (somewhat less commonly) "spillover" of adults or larvae into adjacent areas has often been observed, these phenomena do not necessarily imply enhanced yields because the additional yield from spillover must be balanced against the direct loss of yield from the closures. The natural variability of recruitment and yield, together with the lack of true controls or replication, make it difficult to empirically determine the effect of long-term closures on yield.

For this reason, models, most of them simulations, have often been used to understand the effects of closures (reviewed in Gerber et al. 2003). It is difficult to infer general principles from simulations, and results can be sensitive to parameter choices. Previous analytic modeling of the effects of closures has typically involved neglecting age structure or some other unrealistic oversimplification. For example, Hastings and Botsford (1999) demonstrated that maximal sustainable yield (MSY) from a conventional effort-based strategy can also be obtained using closures with infinite fishing mortality in the open areas. However, yield was measured in numbers caught, rather than weight. Because the mean age of the catch is greater in the conventional MSY policy, the catch in weight will usually be greater with the effort-based strategy than with their marine reserve approach.

The purpose of this article is to develop an analytical age-structured approach for analyzing the effects of long-term closures. It is an extension of the ideas from Beverton and

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Fig. 1. Yield as a function of fishing mortality and closure fraction for (*a*, *c*, *e*, *g*) canary rockfish (*Sebastes pinniger*) and (*b*, *d*, *f*, *h*) Georges Bank sea scallop (*Placopecten magellanicus*). (*a*–*b*) Equilibrium yield as a function of fishing mortality for closure fractions 0 (solid line), 0.1 (broken line), 0.4 (dashed–dotted line), and 0.7 (dotted line). (*c*–*d*) Yields as a function of closure fraction for various fishing mortalities (for canary rockfish, $F = 0.05$ (solid line), 0.15 (broken line), 0.3 (dashed–dotted line), 0.5 (dotted line); for sea scallop, $F = 0.24$ (solid line), 0.6 (broken line), 1.2 (dashed–dotted line), 2.0 (dotted line)). (*e*–*f*) Surface plots of yield. (*g*–*h*) Yield gradient fields (arrows, fifth root transformed) and yield isopleths (solid lines); the shaded area indicates the portion of the (F, C) plane where an increase in the closure fraction increases yields, according to eq. 15. The two arrows on the abscissa indicate (left to right) F_{MSY} and $F_{\max}$, the fishing mortalities that maximize sustainable yield and yield per recruit, respectively. Note that the fishing mortality that produces maximal yield at a given closure fraction C increases for canary rockfish and approaches $F_{\max}$ at high closure fractions. This optimal fishing mortality for sea scallop is nearly constant with C because the stock–recruitment function is almost completely saturated at $F_{\max}$, so that $F_{\max} \approx F_{\text{MSY}}$.

Holt (1957) and Shepherd (1982), who combined per recruit and stock–recruitment curves to calculate yield.

Model development and results

Yield can be expressed as

$$(1)\qquad Y = yR$$

where y is yield per recruit and R is recruitment (Beverton and Holt 1957; Shepherd 1982; Quinn and Deriso 1999). Recruitment at spawning stock biomass (SSB), B, is determined through a stock–recruitment relationship $R = s(B)$. At equilibrium, recruitment is implicitly defined by the equation

$$(2)\qquad R = s(B) = s(bR)$$

where b is SSB per recruit. Here, egg production, perhaps adjusted for the viability of the eggs, could be substituted for SSB, in which case b would represent eggs per recruit. It will be assumed through eq. 15 that recruitment is positive at the equilibrium of interest (i.e., the R satisfying eq. 2 is positive), and that at this equilibrium,

$$(3)\qquad |bs'(bR)| < 1$$

where s' represents the derivative of s with respect to B. This condition (eq. 3) will assure that in the dynamical system defined by

$$(4)\qquad R_{n+1} = s(bR_n)$$

the equilibrium solution (eq. 2) is attracting (i.e., asymptotically stable; Hale and Koçak 1991); it will be satisfied by nonzero equilibria under most realistic conditions. Of course, the system is never exactly in equilibrium, but it will tend to return towards an attracting equilibrium after a perturbation, so that an equilibrium analysis will give insights into the dynamics of the system.

It will be assumed that adults are sufficiently sedentary so that exchange of adults between open and closed areas is negligible, but that larvae are well mixed between the open and closed areas. Let C be the fraction of recruitment that occurs in areas closed to fishing. Because recruits in the closures produce no yield, the mean yield per recruit (y) and SSB per recruit (b) with closures at fully recruited fishing mortality F are given by

$$(5)\qquad y = (1 - C)y_0(F)$$

and

$$(6)\qquad b = Cb_0(0) + (1 - C)b_0(F)$$

where y_0 and b_0 are yield per recruit and SSB per recruit without closures. To simplify notation, y and b will represent yield and SSB per recruit at fishing mortality F and closure fraction C, i.e., $y = y(F, C) = (1 - C)y_0(F)$ and $b = b(F, C) = Cb_0(0) + (1 - C)b_0(F)$. Fishing mortality rates will always be calculated with respect to the fished area only.

Equations 1 and 2 implicitly define yield Y as a function of fishing mortality F and the fraction closed C. The partial derivatives of Y with respect to these quantities are

$$(7)\qquad \frac{\partial Y}{\partial F} = \frac{\partial y}{\partial F}R + y\frac{\partial R}{\partial F} = (1 - C)\left[y_0'(F)R + y_0(F)\frac{\partial R}{\partial F}\right]$$

and

$$(8)\qquad \frac{\partial Y}{\partial C} = \frac{\partial y}{\partial C}R + y\frac{\partial R}{\partial C} = \frac{\mathrm{d}(1 - C)}{\mathrm{d}C}y_0(F)R + (1 - C)y_0(F)\frac{\partial R}{\partial C}$$
$$= y_0(F)\left[(1 - C)\frac{\partial R}{\partial C} - R\right]$$

The partial derivatives of R can be computed from eq. 2 by implicit differentiation, i.e., by differentiating both sides of eq. 2 and then solving for the derivative of R:

$$(9)\qquad \frac{\partial R}{\partial F} = \frac{s'(bR)\dfrac{\partial b}{\partial F}R}{1 - s'(bR)b} = (1 - C)\frac{s'(bR)b_0'(F)R}{1 - s'(bR)b}$$

and

$$(10)\qquad \frac{\partial R}{\partial C} = \frac{s'(bR)\dfrac{\partial b}{\partial C}R}{1 - s'(bR)b} = \frac{s'(bR)[b_0(0) - b_0(F)]R}{1 - s'(bR)b}$$

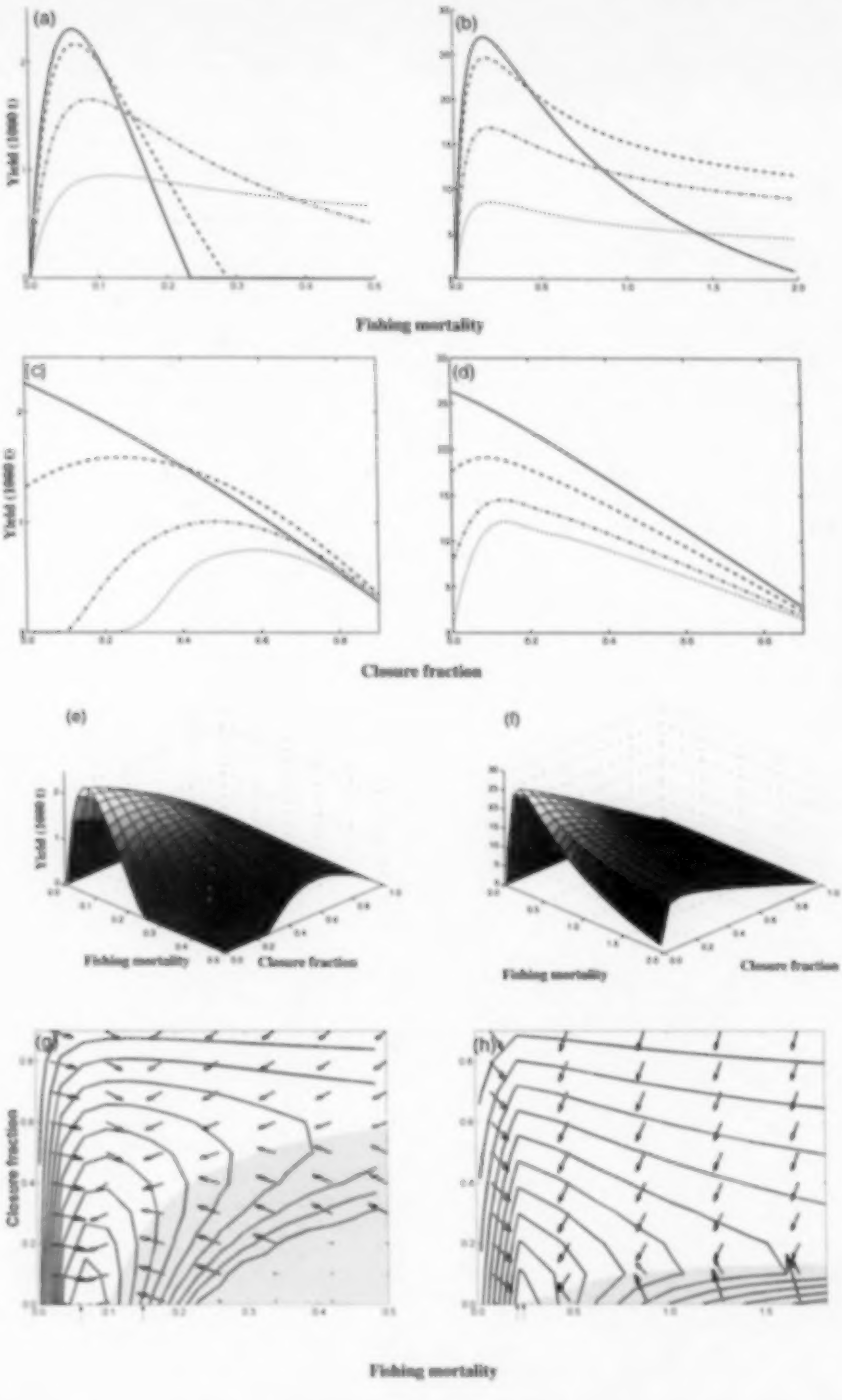
Setting $B = bR$ and substituting eqs. 9 and 10 back into eqs. 7 and 8 gives

$$(11)\qquad \frac{\partial Y}{\partial F} = (1 - C)R\left[y_0'(F) + y_0(F)\frac{s'(B)(1 - C)b_0'(F)}{1 - s'(B)b}\right]$$

and

$$(12)\qquad \frac{\partial Y}{\partial C} = y_0(F)R\left[\frac{(1 - C)s'(B)[b_0(0) - b_0(F)]}{1 - s'(B)b} - 1\right]$$

Equations 11 and 12 allow computation of the gradient of Y, $\nabla Y = \left(\dfrac{\partial Y}{\partial F}, \dfrac{\partial Y}{\partial C}\right)$, that points in the direction of the steepest ascent of yield on the (F, C) plane.



As example applications, the theory is applied here to canary rockfish (*Sebastes pinniger*) and Georges Bank sea scallop (*Placopecten magellanicus*) (Fig. 1; Table 1). Both of these cases are given for the purposes of illustration; the stock–recruitment relationship for Georges Bank sea scallops is uncertain, and movement of adult canary rockfish is neglected in this analysis. These examples nonetheless illustrate and contrast a low productivity species (canary rockfish) that is prone to recruitment overfishing with a highly productive and fecund species (sea scallops) that has a stock–recruitment function that is nearly saturated at $F_{\max}$, the fishing mortality that maximizes yield per recruit. In

Table 1. Parameter estimates and other key quantities for canary rockfish (*Sebastes pinniger*) and Georges Bank sea scallop (*Placopecten magellanicus*).

								C_{crit}		
Stock	α	β, kg	F_{MSY}	F_{max}	$h_B(0)$, kg/recruit	$s'(0)$, recruits/kg	B_c, kg	No exchange	10% exchange	20% exchange
Canary rockfish	9.6×10^6	6.7×10^6	0.06	0.15	1.37	1.4	2.7×10^6	0.51	0.70	0.91
Sea scallop	1.6×10^9	1.4×10^7	0.18	0.22	0.245	112	5.9×10^7	0.036	N/A	N/A

Note: Stock–recruitment functions were specified by the Beverton–Holt parameters α and β, where $s(B) = \alpha B/(\beta + B)$. The stock–recruitment parameters and per recruit calculations for canary rockfish were based on Methot and Stewart (2005), assuming that most of the catch is taken by commercial trawlers; the sea scallop per recruit estimates are from Hart (2003). An attempt to fit a Beverton–Holt curve to scallop stock–recruitment data from 1982–2005 gave a reliable estimate of the asymptote α but could not accurately estimate β because of high recruitment variability together with limited increases in mean recruitment as SSB has increased. Because the Georges Bank sea scallop stock–recruitment relationship appears to be at least partially saturated during the entire observed period, β was estimated as the lowest observed spawning stock biomass (SSB) in the time series. F_{max} and F_{MSY} are the fishing mortalities (with no closures) that maximize yield per recruit and equilibrium yield, respectively. B_c is the SSB for which $s'(B_c) = 1/h_B(0)$, so that closures increase yield below, but not above, this biomass at equilibrium. C_{crit} is the fraction of closure required to prevent stock collapse regardless of fishing mortality or selectivity. For canary rockfish, this quantity is computed assuming that adult exchange between closed and open areas is 0%, 10%, and 20%. N/A, not applicable.

both cases, closures increase yield (indicated by the shaded area and upward slants of the gradients in Figs. 1*g*–1*h*) only at low biomasses corresponding to overfished conditions, and MSY over all *F* and *C* occurs at the conventional F_{MSY} with no closures.

It is of particular interest to determine under what conditions $\frac{\partial Y}{\partial C} > 0$, so that yield increases with greater closure. According to eq. 12, this occurs when

$$(13)\qquad 1 < \frac{(1 - C)s'(B)[h_B(0) - h_B(F)]}{1 - s'(B)b}$$

Multiplying both sides of eq. 13 by $1 - s'(B)b$ (note that by eq. 3, this quantity is positive) and then adding $s'(B)b$ to both sides gives

$$\begin{aligned}(14)\qquad 1 &< s'(B)\{(1 - C)[h_B(0) - h_B(F)] + b\}\\ &= s'(B)[(1 - C)h_B(0) - (1 - C)h_B(F)\\ &\qquad + Ch_B(0) + (1 - C)h_B(F)]\\ &= s'(B)h_B(0)\end{aligned}$$

Thus, $\frac{\partial Y}{\partial C} > 0$ if and only if

$$(15)\qquad s'(B) > \frac{1}{h_B(0)}$$

Intuitively, the increase in recruitment from a marginal increase in the closure fraction, which depends on the slope $s'(B)$ and on SSB per recruit at the origin, must be great enough to compensate for that lost to the additional closure. For typical stock–recruitment curves, an incremental increase in the fraction closed is more likely to increase yield at high fishing mortalities and at low closure fractions, as these factors imply a small *B* and hence a relatively large $s'(B)$. Moreover, for any stock that will not go extinct at zero fishing mortality, $s'(0) > 1/h_B(0)$ (Shepherd 1982), so that eq. 15 must be satisfied at sufficiently low biomass. Thus, eq. 15 gives theoretical insights into the results of numerous simulations that indicate that closures will typically increase yield under overfished conditions, but not when fishing mortality is small.

The formalism described here can answer another important question considered by Mangel (1998) using an aggregate biomass dynamics model: how much closure is necessary to prevent extinction (at equilibrium) at a given fishing mortality *F*? To assure population persistence, the $R = 0$ solution to eq. 2 must be repelling (unstable) in the dynamical system defined by eq. 4. This will occur when

$$(16)\qquad b|s'(0)| > 1$$

(Hale and Koçak 1991).

Solving for $s'(0)$ and assuming that $s'(0) > 0$ (which is always true in any realistic case), the population is assured of not going extinct when

$$(17)\qquad s'(0) > \frac{1}{Ch_B(0) + (1 - C)h_B(F)}$$

Solving eq. 17 for *C* shows that the closure fraction *C* will be sufficient to prevent stock collapse if $C > C_{crit}(F)$, where

$$(18)\qquad C_{crit}(F) = \frac{1/s'(0) - h_B(F)}{h_B(0) - h_B(F)}$$

If $h_B(F)$ is negligible, as is likely the case at very high fishing mortalities, this simplifies to $C_{crit} = \frac{1}{h_B(0)s'(0)}$.

These ideas can be generalized to allow for some types of adult movement. If adults are emigrating out of the closed area at a rate *E* and they do not contribute to spawning after emigrating, then *E* represents a loss to the closed area population entirely analogous to fishing mortality. Thus, closed area SSB per recruit under these assumptions is given by $Ch_B(E)$, and the population will not go extinct if

$$(19)\qquad s'(0) > \frac{1}{Ch_B(E) + (1 - C)h_B(F)}$$

Discussion

The analytic and graphic techniques derived here give simple methods for predicting the effects of closures on yield and stock persistence. They explicitly show the tradeoff between the direct loss of yield from the closures and the increase in yield obtained by recruitment spillover. Although the former is simply a fixed fraction of the total yield, the latter depends on the increase in SSB per recruit from the closures and the slope of the stock–recruitment relationship (see eq. 15).

It has been assumed that density dependence occurs only in the early life history of the target species and so is reflected in the stock–recruitment function only. The predicted yields with closures may be overestimated if there was a reduction of growth or increase in natural mortality of adults due to density dependence in the closures (Gårdmark et al. 2006). On the other hand, an Allee effect, such as density-dependent fertilization success that often occurs in broadcast spawners, could cause the calculated benefits of closures to be underestimated. The assumption of a "well-mixed" larval pool would cause the model with closures to overestimate yield if larvae released in the closed area were more likely to stay in the closed area but it would underestimate yields if the larvae spawned in closed areas tended to be transported to open areas (Gaines et al. 2003; Gårdmark et al. 2006).

Although the criterion for increased yield (eq. 15) was derived under the assumption of no adult mixing between closed and open areas, moderate adult movement should produce qualitatively similar results. The effect of closures in this case would be to create more variability in fishing mortality among individuals in the stock, with some animals remaining in the closed area (and thus subject to zero fishing mortality), others always in the open areas (subject to full fishing mortality), and the remainder spending some time in both open and closed areas (with reduced, but not zero, fishing mortality). Similar to the effect of closures on sedentary stocks, the net effect is to increase SSB per recruit and, except possibly at high fishing mortalities, reduce yield per recruit (Hart 2001). Thus, the effect on SSB and yield per recruit for stocks of moderate mobility is qualitatively similar to that computed here for sedentary stocks, though the effects should be less than those predicted by eqs. 5 and 6.

The evidence presented here and in most other models indicates that long-term closures are unlikely to increase yield when open area fishing mortality is at or less than that which produces MSY (Gerber et al. 2003; Gårdmark et al. 2006). On the other hand, closures can increase yield at high fishing mortalities, prevent stock collapse, and have other conservation benefits (e.g., for biodiversity). They also can serve as useful controls for scientific research purposes. Expectations of marine reserves and other long-term closed areas should focus on these benefits, rather than a hope that they can contribute to optimal yield.

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Effects of silt and very fine sand dynamics in Atlantic salmon (*Salmo salar*) redds on embryo hatching success[1]

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Abstract: We conducted a 2-year field experiment examining the survival to hatching of Atlantic salmon (*Salmo salar*) in relation to the seasonal and spatial variations of silt and very fine sand (SVFS; <0.125 mm) content within a large set of artificial redds at two spawning sites of the Sainte-Marguerite River, Quebec, Canada. Each artificial redd consisted of an infiltration cube (30 cm × 30 cm × 20 cm) buried in a morpho-sedimentological unit resembling a salmon redd. One hundred fertilized Atlantic salmon eggs were inserted in a number of infiltration cubes during redd construction. The results indicate no significant relation between survival to hatching in spring and values of the sand index or total percent fine sediment <2 mm in redds at that time. However, the proportion of SVFS in the redds explained 83% of the variation in embryo survival, with a threshold at approximately 0.2% SVFS, above which survival dropped sharply below 50%. Infiltration of these very fine fractions mostly occurred under ice cover, during the low-flow winter period. However, during the spring flood period, infiltration–flushing patterns varied spatially and reflected spatial differences in local intensity of bed-load transport and fine sediment availability.

Résumé : Une expérience de terrain de deux ans nous a permis d'examiner la survie jusqu'à l'éclosion de saumons atlantiques (*Salmo salar*) en fonction des variations saisonnières et spatiales des quantités de limon et de sable très fin (SVFS, <0,125 mm) dans un important réseau de nids artificiels à deux sites de reproduction de la rivière Sainte-Marguerite, Québec, Canada. Chaque nid artificiel consiste en un cube d'infiltration (30 cm × 30 cm × 20 cm) enfoui dans une unité morpho-sédimentologique ressemblant à un nid de saumon. Nous avons introduit cent oeufs fécondés de saumon atlantique dans plusieurs des cubes d'infiltration durant la construction des nids. Nos résultats indiquent qu'il n'y a pas de relation significative entre la survie jusqu'à l'éclosion au printemps et les valeurs de l'indice de sable, ni avec le pourcentage total de sédiments fins <2 mm dans les nids à ce moment. Cependant, la proportion de limon et de SVFS dans les nids explique 83 % de la variation de la survie des embryons, avec un seuil d'environ 0,2 % de SVFS au-dessus duquel la survie tombe rapidement sous 50 %. L'infiltration de ces fractions très fines se fait surtout sous la glace durant la période d'étiage d'hiver. Cependant, durant la période de crue printanière, les patrons d'infiltration et de curage varient d'un endroit à l'autre en fonction des différences spatiales de l'intensité de la charge de fond transportée et de la disponibilité des sédiments fins.

[Traduit par la Rédaction]

Introduction

Numerous laboratory and field studies have shown that the presence of excessive amounts of fine sediment in salmonid spawning gravels is detrimental to the survival of incubating embryos (see reviews of Chapman 1988; Reiser 1999; and Armstrong et al. 2003). However, the nature and severity of this impact depends on the precise size distribution of the infiltrated fine fraction (Acornley and Sear 1999). While coarse sand may form a seal at the surface of the redds, which decreases the emergence success of fry (Beschta and Jackson 1979; Crisp 1993), finer sand infiltrates deeper in the redds where it negatively affects embryo survival by reducing substrate permeability and the intragravel flow necessary for the oxygenation of the eggs (Turnpenny and Williams 1980; Peterson and Metcalfe 1981; Reiser and White 1988).

Although it is well documented that silt (<0.0063 mm) reduces substrate permeability much more than sand (Vukovic and Soro 1987; Rehg et al. 2005), the potential effect of the

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silt fraction on embryo survival has only recently been considered. Lapointe et al. (2004) have shown in laboratory incubations of Atlantic salmon (*Salmo salar*) embryos that a unit weight of silt is on average three times as detrimental to embryo survival than a similar weight of sand and that survival could be seriously reduced at silt levels as low as 1.5%. In a field experiment examining the relationship between survival of Atlantic salmon embryos contained in incubation baskets and the characteristics of fine sediment infiltrated within the baskets during incubation, Julien and Bergeron (2006) showed that survival to pre-eyed and eyed stages of development were most strongly affected by silt, although this size fraction always represented less than 0.8% of the grain size distributions inside the incubation baskets.

However, despite the growing interest concerning the potential negative effect of silt on the quality of spawning gravels (Acornley and Sear 1999; Armstrong et al. 2003), field data documenting the sensitivity of salmonid embryos to this very fine size fraction are still scarce, and very little is known about the spatial and temporal dynamics of silt in redds of gravel bed salmon rivers. Payne and Lapointe (1997) proposed that the lateral position of redds with respect to the high- and low-flow velocity zones found across a riffle has an effect on the probability of sand accumulation in redds. However, because the source zones and transport behaviour of silt may differ qualitatively from those of sand, it is unclear whether such spatial patterns apply to silt infiltration over spawning zones. There is also a lack of information concerning the temporal variations of silt within redds, despite the fact that it has been recognised that the precise timing of fines infiltration may be important in determining reproductive success (Kondolf 2000). For example, Reiser and White (1988) suggested that there could be higher mortality associated with fine sediment accumulation occurring in early embryonic development stages compared with the stages after the circulatory process becomes functional.

Finally, the dynamics of fine sediment infiltration in ice-covered streams is poorly documented. In most Atlantic salmon rivers, a large portion of the embryo incubation period coincides with winter low-flow conditions and the presence of an ice cover. Although occasional warm winter spells can lead to ice breakup, jamming, and local scour, the most common effect of an intact ice cover is to reduce flow velocity through an increase of resistance to flow, thereby decreasing sediment transport capacity over both riffles and pools (Beltaos et al. 1993; Prowse 1994). Thus, the ice cover period should be most suitable for the infiltration of fine sediment into spawning gravels. However, this specific phenomenon has never been studied.

The general aims of this study were to document the seasonal and spatial variations of fine sediment among a large set of artificial Atlantic salmon redds in two sites of an ice-covered river and to quantify the impact of these variations on embryo survival. More specifically, the study intended to (*i*) assess the relative variability in time and space of artificial redd content in medium and coarse sand (0.125–2 mm) compared with very fine sediment fractions (<0.125 mm); (*ii*) determine the relative importance of these size fractions as predictors of salmon embryo survival to hatching; (*iii*) determine the nature of seasonal variations in infiltration of very fine fractions in salmon redds; and (*iv*) investigate to what extent potential silt infiltration is controlled by redd location within the channel.

Materials and methods

Study sites

The study was conducted on the Principale branch of the Sainte-Marguerite River (SMR) in the Saguenay region, Quebec. This gravel–cobble bed river, which supports Atlantic salmon and brook trout (*Salvelinus fontinalis*) populations, drains a Canadian Shield catchment of 1500 km^2 dominated by coniferous forests. A stable ice cover is generally present on the river from mid-November to the end of March. Peak discharge typically occurs between March and mid-May after ice breakup. The bank-full width of the channel is approximately 45 m near the river mouth, where bank-full discharge is approximately 110 m^3·s^{-1}.

Two distinct riffle sections used by Atlantic salmon for spawning were chosen as study sites. The Glass Pool site is located 41.2 km from the mouth and has been the most intensely used spawning riffle on the main branch of the SMR over the past decade. In contrast, the once important Bras des Murailles spawning site, located 49.7 km from the mouth, has been degraded over the 1970s and 1980s by increased sand content in local substrate tied to increasing sediment production from a large-scale, anthropogenic meander rectification upstream (Talbot and Lapointe 2002*a*, 2002*b*). At 21.8 mm, the median bed surface (pavement) particle size (D_{50}) at the Bras des Murailles site is finer than that at Glass Pool (28.7 mm). Mean subpavement sand content of Glass Pool riffle substrate is under 15%, while it exceeds 25% in certain zones within the Bras des Murailles site. The morphology and hydraulics of the Glass Pool site is that of a classic riffle bar set between two oppositely curved river bends with deep pools (Fig. 1*a*). In contrast, the Bras des Murailles site is much less sinuous and a large, abandoned oxbow lake reconnects with the SMR a few metres upstream of the study site (Fig. 1*b*).

Fine sediment infiltration and embryo survival measurements

The general approach was to obtain, for two consecutive incubation periods (2000–2001 and 2001–2002), concurrent field measurements of fine sediment content and Atlantic salmon embryo survival in artificial redds. We wanted to replicate, as closely as possible, the morphology and grain size composition of natural salmon redds, as well as the flow and sediment transport conditions experienced by embryos in natural redds during the incubation period.

Artificial redd construction

Using the method described in Levasseur et al. (2006), each artificial redd consisted of an infiltration cube containing a known amount of fertilized eggs and buried in a morpho-sedimentological unit resembling a salmon redd. The infiltration cube method is a modification of the infiltration bag sampling method described by Lisle and Eads (1991). An infiltration cube was made up of a rectangular (30 cm × 30 cm × 20 cm) steel frame with no walls, which

Fig. 1. Plan view of (*a*) Glass Pool and (*b*) Bras des Murailles study sites with positions of artificial redd patches in year one (white circles) and in year two (solid circles). Arrows indicate the direction of flow at each site.

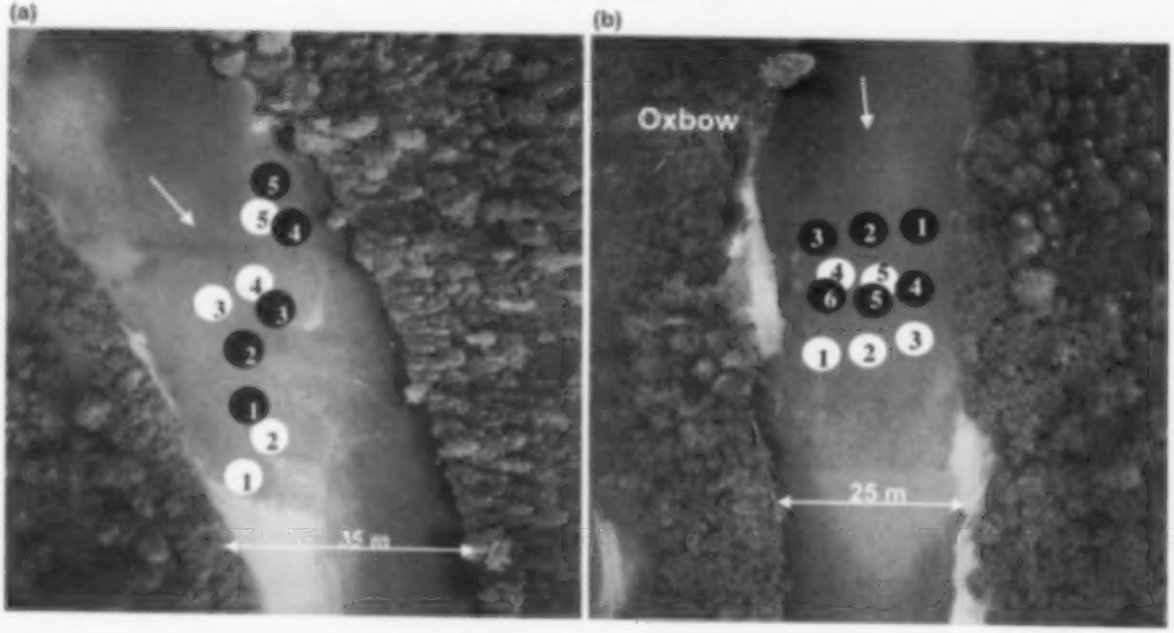
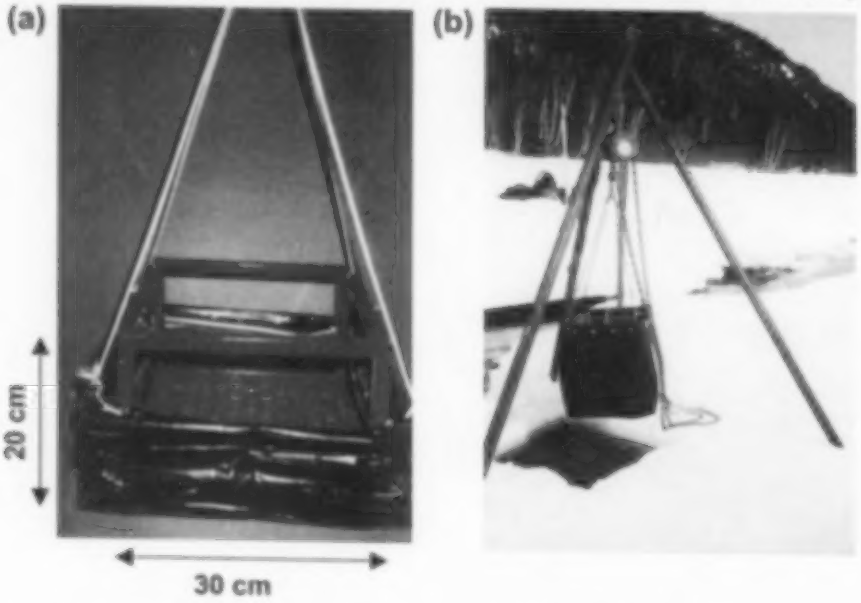


Fig. 2. (*a*) An infiltration cube with the folded bag attached to its base. (*b*) Extraction of an infiltration cube during winter.



had a folded plastic bag attached to its base (Fig. 2*a*). Four wires were affixed to the corners of the bag and projected above the bed surface after installation for later removal. These wires were used to raise the sides of the watertight bag and winch it up along with the substrate contained by the cube using a tripod installed on the river bed or ice surface (Fig. 2*b*). The infiltration cube provided a quick, easy, and robust method to pull relatively large samples (~65 kg), yielding more precise grain size statistics, out of underwater substrate even during tough winter field conditions. The cube design also precluded bias in infiltration rates by both allowing lateral sediment transport within substrate (absence of walls on the cube) and preventing loss of fine particles during retrieval from underwater. Each infiltration cube was buried in the substrate using a procedure aimed at reproducing a natural salmon redd. First, a depression about 30 cm deep and 75 cm wide was dug in the substrate by manually excavating the particles underwater and pushing them downstream of the current. The infiltration cube was then installed in the depression and buried by mobilizing particles from the bed just upstream in a manner similar to a spawning female salmon. This enabled fine sediments to be swept downstream by the flow, thereby constructing a redd composed of coarser lag gravels with fewer fines and larger pore sizes than outside the redd. Upon completion, each artificial redd therefore had the typical grain size and form characteristics of a natural salmon redd with an upstream pit and a downstream tailspill. Each artificial redd was paired with a circular bed-load trap (diameter 15 cm; depth 20 cm) buried flush with the bed surface. Each trap, initially installed empty with a cover, was activated by removing its cover, thereby enabling bed-load sampling for a predetermined period of time.

Spatial and temporal sampling design

Because current field techniques do not allow accurate determination of fine sediment content within redds in a way that is nondestructive of redd structure and function, it is currently not possible to directly determine the temporal variation of fine sediment content of a single redd through repeated observations of that redd. For this reason, we devised an approach that assesses temporal variation in redd fine sediment content at the local scale by monitoring a set of replicate artificial redds laid out within a relatively small (~4 m diameter), homogenous area of spawning habitat, called a patch. Within each patch, a group of five to six artificial redds were installed, in similar water depth, flow velocity, and bed substrate conditions, immediately following the spawning period of Atlantic salmon (late October in SMR). Infiltration cubes and bed-load traps within each patch were then extracted sequentially for grain size analysis at five periods during the incubation period. At the time of installation in October, one infiltration cube per patch was removed immediately following installation to quantify the initial proportion of fines in the artificial redds of each patch at time zero. At the same time, the sediment trap associated with the next infiltration cube to be extracted was activated. Then, an infiltration cube and its associated bed-load trap were removed from each patch at each of the four other sampling periods: in December during low-flow winter conditions, just prior to ice formation; in January following the formation of a solid ice cover; in late March prior to ice breakup; and in late May or June after the spring flood. We used the difference in fines content between successively extracted cubes within the same patch as our best estimate of the temporal change in fines content over the period at this patch.

To capture the spatial variation of fine sediment infiltration or flushing at each site, five to six of these patches were laid out to range both laterally across and along each spawning area (Figs. 1*a*, 1*b*). All patches were carefully delimited so that they were small enough to be homogenous in terms of water depth, flow velocity, and substrate size. The sampling design thus included two sites over 2 years, with five to six patches per site each containing five to six cubes (N = 116 cubes over 2 years). Note that newly installed cubes (in October) did not have uniform sedimentology across patches or sites. They rather collectively represented a large sample of fresh spawning redds incorporating natural variations due to variable spawning conditions along the river.

Grain size analysis

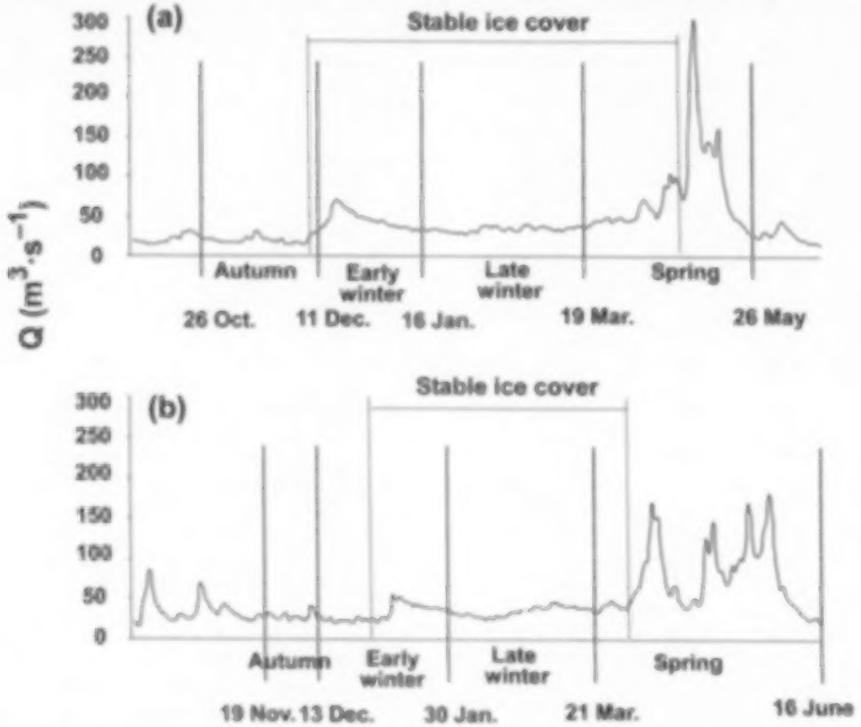
The coarser part of the sample recovered from each infiltration cube (particle sizes >16 mm) was wet-sieved and weighed in the field, and a well-mixed subsample of the <16 mm fraction was taken in the laboratory for a standard dry sieve analysis at 1 phi intervals (phi = $-\log_2 D$). This study focused on the fine sediment content of each cube (as a weight percentage of the entire sample) for four grain size fractions: medium–coarse sand (MCS, 0.250–2 mm), fine sand (FS, 0.125–0.250 mm), very fine sand (VFS, 0.063–0.125 mm), and silts (SILTS, <0.063 mm).

Embryo survival

Embryo survival was studied by inserting, at artificial redd construction, 100 fertilized Atlantic salmon eggs in some of the infiltration cubes of each patch. In 2000–2001, one of the five cubes installed contained eggs, while in 2001–2002, two of the six cubes installed contained eggs. The eggs and milt were obtained from the Tadoussac hatchery. The eggs were of the same genetic stock as the Atlantic salmon adults native to the SMR. The eggs were fertilized and water-hardened at the hatchery (located ~25 km away from the river) and then transported to the field in cool, water-filled jars. The eggs were kept at the same temperature as the stream water to avoid thermal shock during artificial redd construction and infiltration cube installation. Within an artificial redd, the eggs were positioned ~20–25 cm below the surface, which is the typical range of burial depths for Atlantic salmon eggs (DeVries 1997). All artificial redds were completed and eggs buried in the substrate within 24 h of fertilization.

The infiltration cubes containing embryos were extracted from the bed when it was determined that the embryos had hatched but prior to emergence to prevent the possible loss of emerging fry. For each year, the hatching period was estimated from hourly temperature data records obtained from temperature data loggers buried within the substrate of each site. At the beginning of May of each year, water temperature data were retrieved from the loggers and used to estimate the progression in the development and hatching dates of the embryos from the degree-day curve for Atlantic salmon published by Ministère Agriculture, Pêcheries et Alimentation Québec (MAPAQ 1996). For both years, it was estimated that by the third week of May, a large proportion of the surviving eggs should have hatched while most of the dead eggs would have not had the time to decompose, thereby allowing the evaluation of mortality. Immediately following extraction, these cubes were carefully inspected using rinsing water to recover and count the number of dead and live embryos. Survival to hatching in an artificial redd was determined by calculating the ratio of recovered hatched fry (dead or alive) to the total number of recovered embryos (fry + dead eggs), as opposed to the number initially buried. While we acknowledge the possibility of overestimating sur-

Fig. 3. Sampling periods and discharge (*Q*) variations during the study periods of (*a*) year one (2000–2001) and (*b*) year two (2001–2002) as measured at the stream gauge number 62803 of the Ministère de l'Environnement du Québec located on the downstream portion of the Nord-Est branch of the Sainte-Marguerite River near its confluence with the Principale branch.



vival as noted by Pauwels and Haines (1994), we prefer this method when the cause of egg disappearance is unknown. Once all embryos and fry from a cube were recovered and counted, the substrate was analyzed for fine sediment content using the procedure described above.

Results

Infiltration cube sampling periods and recovery success

The infiltration cube sampling periods varied slightly between years because of environmental factors. In year one, because of early ice formation, the infiltration cubes that we planned to retrieve prior to ice cover formation were instead recovered just after a stable ice cover had formed (Fig. 3*a*). In year two, persistent high water levels in the spring prevented the timely recovery of the infiltration cubes containing the hatched embryos (Fig. 3*b*). These cubes were thus recovered 16 June in year two compared with 26 May in year one.

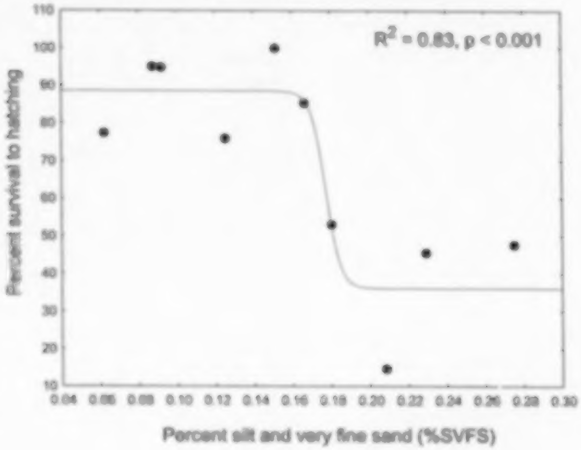
Of the 116 infiltration cubes that were installed in both years combined, only four were not recovered, representing an overall recovery success of 97%. In year one of the study (2000–2001), three cubes could not be recovered as planned because they were frozen in the riverbed. In year two (2001–2002), one cube was washed away from the bed during the spring flood. The recovery success of the bed-load traps was also very good. None of the 40 traps were lost in year one, while 4 of the 55 traps of year two were lost, all of them being scoured away from the Glass Pool site during the spring flood. However, many bed-load traps completely filled with sediments during both spring floods, despite the fact that larger traps were used for year two. Therefore, bed-load transport rates could not be reliably estimated, and it was decided to use the size of the largest particle found in each trap as an index of local flow competence.

The embryo recovery success was good in year one (64.8%) but poor in year two (38.7%). It is likely that the protracted spring flood of year two incited some of the pre-emerging fry to leave the redds to avoid being crushed by pavement mobilization or that they were simply scoured away. Because of the poor embryo recovery success of year two, only data from year one were considered in the remaining embryo survival analysis. However, data from both years were used in the analysis of the fine sediment content dynamics of the artificial redds.

Effect of fine sediment on survival to hatching

Large variations in percent survival to hatching were observed across the artificial redds (mean 69.0%, range 14.8%–100%). However, these variations failed to correlate significantly ($p > 0.05$) with simple extant metrics of overall fine contents, such as the Peterson and Metcalfe's (1981) sand index (SI) and the total percent fine sediment <2 mm, despite the existence of large variations in sand content (percentage <2 mm) across all redds sampled (mean 13.2%, range 0.4%–27%). We therefore pursued the analysis by

Fig. 4. Relation between the percentage of silt and very fine sand in redds (%SVFS) and the percent survival to hatching of Atlantic salmon (*Salmo salar*) embryos. % survival = 36.09 + 54.49/[1 + exp[(%SVFS – 0.17728)/0.0037]].



subdividing the overall fine sediment <2 mm into four fractions: percent MCS, percent FS, percent VFS, and percent SILTS. While MCS did not correlate significantly ($p > 0.05$) with survival, FS, VFS, and SILTS all showed significant ($p < 0.05$) negative correlations with percent survival to hatching, with respective R^2 values of 0.3, 0.6, and 0.5. However, because the two finest fractions (VFS and SILTS) were strongly intercorrelated in our data set ($R^2 = 0.9$, $p < 0.0001$), their independent effects on survival could not be separated by a multiple regression analysis. This compelled us to examine the dependency of embryo survival on the percentage of VFS and SILTS combined, a fraction (<0.125 mm) we called silt and very fine sand (SVFS). There was a strong significant relation ($R^2 = 0.83$, $p < 0.001$) between these two variables (Fig. 4). This relationship, which appears to have a negative logistic form, showed a threshold at 0.2% of SVFS over which survival drops sharply below 50%. Multiple regression analysis demonstrated that once SVFS was included in the model, FS did not add significantly ($p < 0.05$) to the prediction of embryo survival to hatching.

To determine the impact of fine sediment content in redds at various sampling moments on embryo survival to hatching, we regressed hatching success data at incubation cubes of a patch against fines content from cubes that had been extracted at previous sampling moments in the same patch (i.e., autumn, early and late winter). This analysis yielded no major relationships between embryo survival and variations of any of the fine fractions over these earlier periods on the same patch.

Fine sediment dynamics

Statistics describing the relative variability of the different fine sediment fractions within the entire artificial redd data set (across all sites, seasons, and years) show a considerable range of fines content (Table 1). Although the absolute variability is greater for the coarser fractions than for the finer ones (e.g., standard deviation (SD) = 5.2 for MCS and 0.13 for SILTS), the finest fractions are relatively more variable (e.g., coefficient of variation (CV) = 40 for MCS and 85 for SILTS). This suggests that the processes driving the dynamics of the coarser and finer fractions in redds differ, and to the extent that the finer fractions are here shown to be biologically significant, the factors controlling this variability in space and time need to be understood.

Table 1. Statistics of the relative variability (standard deviation (SD) and coefficient of variation (CV)) in the different fine sediment fractions within the entire data set (all cubes, all sites, all periods, and all years).

	Sediment fraction (%)				
Statistic	<2 mm	MCS	FS	VFS	SILTS
SD	5.3	5.2	0.08	0.32	0.13
Mean	13.2	12.3	0.11	0.70	0.16
CV	40	42	77	46	85
Minimum	0.4	0.4	0.02	0.12	0.04
Maximum	27	26	0.5	1.6	0.72

Note: MCS, medium–coarse sand (0.250–2 mm); FS, fine sand (0.125–0.250 mm); VFS, very fine sand (0.063–0.125 mm); SILTS, silts (<0.063 mm).

Seasonal patterns in SVFS content

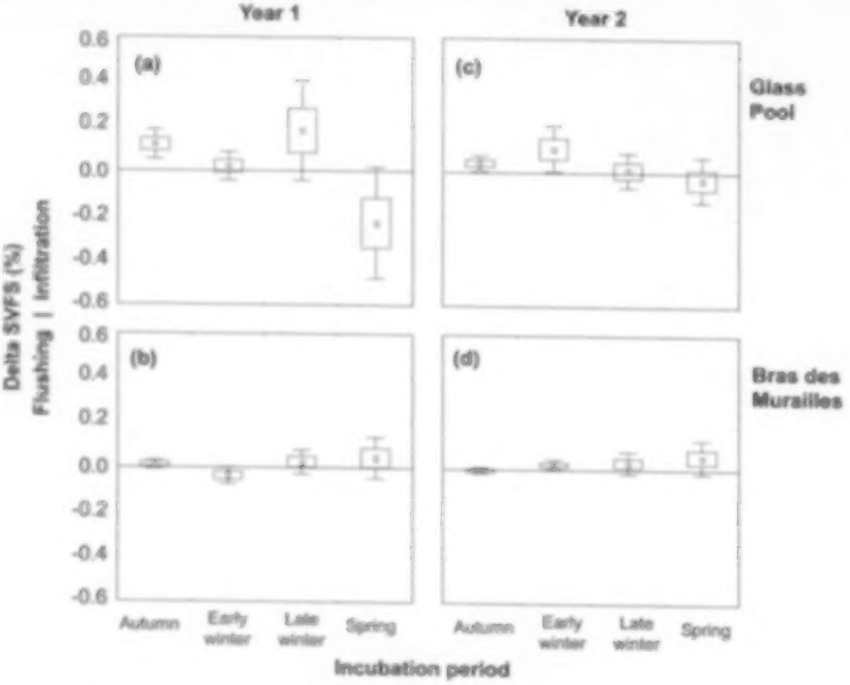
The seasonal evolution of SVFS, the fraction that best explained embryo survival data, showed relatively coherent temporal patterns of infiltration and flushing in the artificial redds (Fig. 5). For both sites and years, there was a systematic tendency for SVFS content in redds to increase during the autumn, early winter, and late winter periods. However, during the spring period, flushing of SVFS dominated in most patches of the Glass Pool site in both years (Figs. 5*a*, 5*c*), whereas infiltration dominated both years in most patches of the Bras des Murailles site (Figs. 5*b*, 5*d*). Although the measured increase or decrease in SVFS content for each period were small, they were well above detection level, since a 0.1% variation in SVFS content represents a change of 60 g in that fraction over a typical 60 kg infiltration cube sample.

Overall, the SVFS content in redds at the Glass Pool site was more variable than that at the Bras des Murailles site, both seasonally as expressed by large variations of the mean between sampling periods and spatially as indicated by larger SD values for any given period (Fig. 5). In some occasions, for example at the Bras des Murailles site during the late winter period (Figs. 5*b*, 5*d*), both infiltration and flushing of SVFS occurred at different redds patches within the same sampling period, possibly reflecting spatial variations in hydraulic and sedimentary conditions dependent on lateral patch location on the site.

Seasonal pattern in bed-load transport competence

An analysis of the seasonal pattern in bed-load transport competence, as measured by the size of the largest particle (D_{max}) found in each bed-load trap, revealed an overall trend of low-intensity bed-load transport during the autumn, early winter, and late winter sampling periods, at both sites and for both sampling years (Fig. 6). During these periods, D_{max}

Fig. 5. Temporal variations of infiltration (positive) and flushing (negative) of silt and very fine sand (SVFS) during the incubation period for both sites and sampling years. Each boxplot shows the mean, standard error, and standard deviation of the difference of SVFS content between two sampling periods for all homogenous patches of a study site.



values were generally much smaller than the D_{50} values of the patches of each site, thereby indicating phase one bed-load transport events. However, in year two, larger flow events caused by strong fall storms (Fig. 3*b*) mobilized particles coarser than the D_{50} at some patches of both sites (Figs. 6*c*, 6*d*). For both sites and years, the spring period was characterized by extreme hydraulic events (Figs. 6*a*, 6*b*) for which D_{max} was greater than D_{50}, indicating phase two bed-load transport events characterized by bed pavement mobilization.

Relation between SVFS and bed-load competence

A comparison of the seasonal patterns of SVFS content in redds (Fig. 5) and of bed-load transport competence (Fig. 6) indicates that periods with low transport competence (autumn, early winter, and late winter) tended to correspond to periods of SVFS infiltration at most redd patches. At the Bras des Murailles site, slight flushing of SVFS was measured during the early winter period of year one and during the autumn period of year two. However, both periods were characterized by bed-load transport events with some D_{max} values exceeding the D_{50} of the bed surface pavement. For both sites and years, the spring period was characterized by very competent flow events (Fig. 3), but the effect on SVFS content in redds differed markedly between sites. While these events were associated with SVFS flushing at the Glass Pool site (Figs. 5*a*, 5*c*), they were related to SVFS infiltration at the Bras des Murailles site (Figs. 5*b*, 5*d*). These results suggest the potential importance of the geomorphic characteristics of the sites and redd location on the relation between bed-load competence and SVFS content in redds.

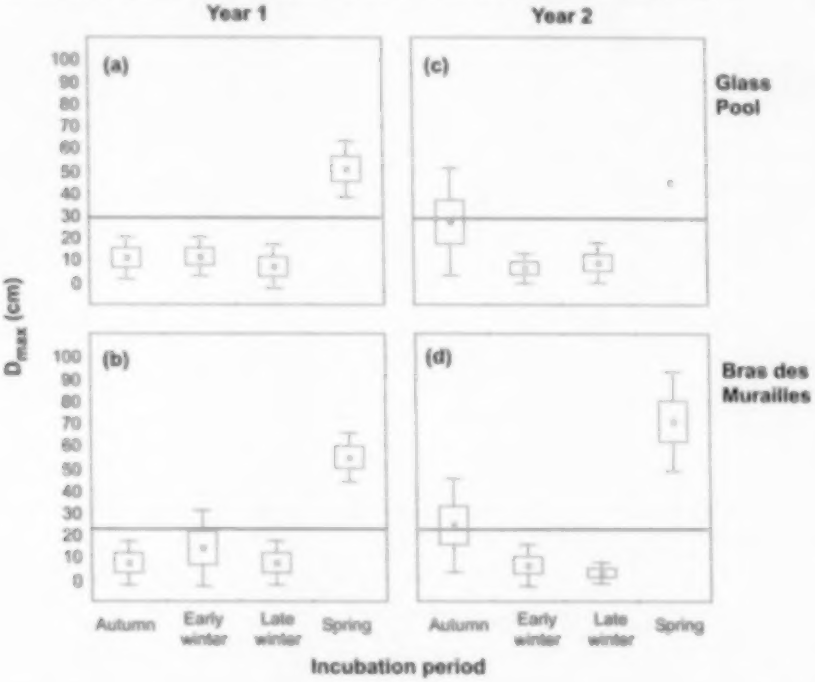
Spatial patterns

A comparison of the temporal patterns of SVFS content between patches of a site for a given year reveals coherent spatial trends between neighbouring patches showing similar geomorphic conditions (Fig. 7). These differences are not readily apparent during the autumn, early winter, and late winter periods because these periods are characterized by a general tendency for SFVS to increase gradually at most redd patches. However, during the spring period, clear groups of patches showing similar SVFS dynamics can be determined.

At the Glass Pool site in year one, patches 4 and 5 (Fig. 7*a*), located on the left side of the channel (Fig. 1*a*), show clear reductions of SVFS over the spring period. In year two, a similar reduction of SVFS occurs at patch 5 (Fig. 7*b*), also located on the left side of the channel (Fig. 1*a*). At the Glass Pool site, the left side of the channel corresponds to the outside of a bend where the flow is deeper and velocities are higher during large flow events.

The situation is more complex at the Bras des Murailles site, where fine sediment accumulates during flood recession at a lateral bar located at the exit of an oxbow along the right bank (Fig. 1*b*). Patch proximity to this fine sand and mud-rich bar seem to control patterns of fines infiltration or flushing in the spring at this site. Fines increased strongly over the spring period at patches 1, 4, and 5 in year one

Fig. 6. Temporal variations of bed-load competence during the studied periods. Each boxplot shows the mean, standard error, and standard deviation of the largest particle size (D_{max}) found in each bed-load trap opened at the beginning and extracted at the end of each sampling period for each site. The horizontal line corresponds to the value of the median bed surface particle size (D_{50}) at the site. This line is useful as an approximate grain size reference to distinguish phase 1 bed-load events (where only fine particles are moving) from phase 2 events (where the bed surface pavement is mobilized). Data points above the line represent more powerful sediment transport events allowing extensive bed substrate mobilization (D_{max} bed load > D_{50} bed), while the lower part is linked with low bed-load transport events not competent enough to allow pavement mobilization (D_{max} bed load < D_{50} bed).



(Fig. 7*c*) and at patches 2 and 6 in year two (Fig. 7*d*), which are all located near the oxbow exit and side bar. Fines decreased at patches 2 and 3 in year one and at patch 4 in year two, which are located in the deeper, more central part of the channel or closer to the left bank, away from this fine sediment accumulation area. These patterns demonstrate the importance of transverse redd location within the study site as a control on the temporal variations of fine sediment present in the substrate during the high-flow period.

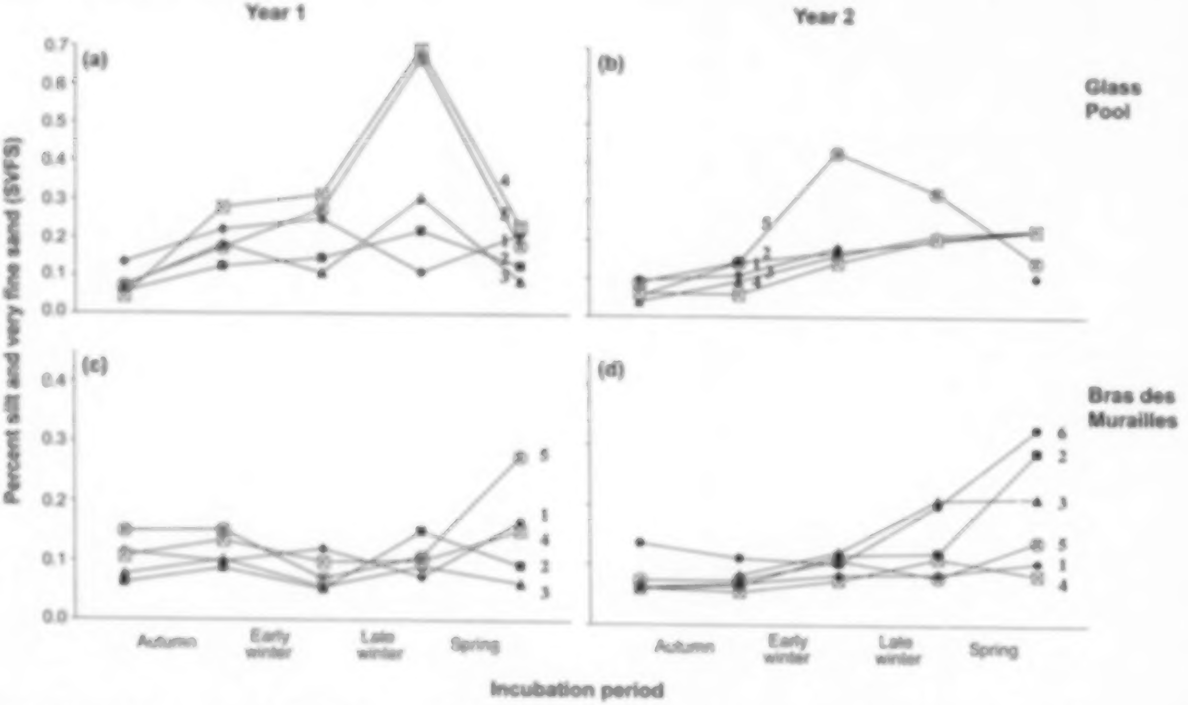
Discussion

Effects of SVFS content on embryo survival

Our results show the important effect on embryo survival of natural variations of even small amounts of SVFS content in Atlantic salmon redds. Although large variations of the traditional SI and sand content spawning substrate quality criterion were present in our data set of the SMR, no significant effect of these variables on survival to hatching was found. However, the proportion of SVFS in the redds explained 83% of the variation in embryo survival to hatching, with a threshold at approximately 0.2% SVFS, above which survival dropped sharply below 50%. This threshold value is broadly consistent with the 0.3%–0.4% silt content value below which survival of Atlantic salmon embryos dropped below 50% in a field experiment by Julien and Bergeron (2006), but it is much smaller than the 1.5% silt content level above which survival to emergence of Atlantic salmon embryos was found to be seriously reduced in a laboratory experiment by Lapointe et al. (2004). This difference is probably due to the difficulty of replicating, in the laboratory, the low values of subsurface hydraulic gradients responsible for driving the flow across the redds in the field. The laboratory study of Lapointe et al. (2004) indeed revealed that the impact of SILTS was stronger at lower hydraulic gradients.

The recent findings of Greig et al. (2005) may provide an explanation for our results by showing an important effect on embryo survival of very small amounts of SVFS. In their laboratory experiment on oxygen consumption by Atlantic salmon embryos approaching hatching, they found that clay-sized sediment created a thin, low permeable seal around the eggs, which restricted the availability of oxygen to the incubating embryos. They also found that clay-sized particles could physically block the micropore canals of the egg membrane, thereby restricting oxygen uptake. The results of Greig et al. (2005) provide a mechanism by which, in our study, very small amounts of SVFS particles may have reduced oxygen availability to the incubating eggs and reduced survival to hatching. In view of these recent findings,

Fig. 7. Temporal variations of silt and very fine sand (SVFS) content at each sampling period for both sites and sampling years. Each point of a line represents the SVFS content of an infiltration cube extracted from the same patch (1–6) at a distinct sampling moment throughout the incubation period. An increase corresponds to infiltration, while a decrease corresponds to flushing of SVFS. Note that scales are different between sites.



it is suggested that sediment fractions finer than those contained in the SI spawning substrate quality criteria need to be taken into account as a sedimentary control in the incubating environment.

Seasonal and spatial dynamics of SVFS

The infiltration cube method employed in this study prevented the loss of SVFS particles during retrieval of the substrate sample from underwater, which allowed the detection of small variations of this fine fraction. Although the proportion of SVFS rarely exceeded 1% of the redd, it was shown to vary seasonally and spatially and to play an important role in determining embryo survival to hatching.

We assumed that within-patch comparisons of cubes extracted at successive times mostly captured temporal variations due to the infiltration or flushing of fine sediment at that patch, with a small random noise effect due to minor spatial variations within the 4 m diameter patch. The validity of this last assumption was confirmed by the coherence of the temporal trends of fine sediment content between neighbouring patches of each study site.

At the two studied spawning sites, the overall pattern of variation of the biologically significant SVFS fraction was of a gradual accumulation at most patches during low flows, especially during the ice-covered winter period. This result supports the suggestion that reduced sediment transport capacity under winter ice cover favours the infiltration of fine sediment into spawning gravels. During the high-flow, pavement-mobilizing events that characterize the spring periods, local controls on the supply of SVFS, as well as flow patterns typical of asymmetric meander cross-sections, appeared to determine the flushing or infiltration of SVFS within the redds. At the Glass Pool site, we observed a pattern of flushing of fines in the redds located towards the outside of the bend and of infiltration in the redds located on the inner side of the bend, near the point bar. This result is consistent with the differential pattern of flushing and infiltration of sand previously observed by Payne and Lapointe (1997) on the high- and low-velocity zones of spawning riffles, respectively. At the Bras des Murailles site, an anomalous oxbow connection just upstream from the spawning site modified these simple spatial patterns by favouring, during flood recession, the accumulation of silt and fine sand on the lateral bar located at the exit of the oxbow. Despite the occurrence of pavement-mobilizing spring flows at this site, SVFS accumulated over that period in most redds located near the oxbow exit and lateral bar, whereas it decreased in redds located in the deeper, more central part of the channel, away from this fine sediment accumulation area. These results suggest that geomorphic controls on local supply and infiltration potential of SVFS may be important factors to be considered for spawning habitat management and conservation in Atlantic salmon rivers.

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Does eel metamorphosis cause a breakdown in the tenets of otolith applications? A case study using the speckled worm eel (*Myrophis punctatus*, Ophichthidae)

Perce M. Powles, Jonathan A. Hare, Elisabeth H. Laban, and Stanley M. Warlen

Abstract: Several basic tenets of otolith research have been questioned recently with regard to eel metamorphosis. Specifically, some researchers have suggested that otolith increment formation is not daily, and otolith material may be resorped during metamorphosis. We conducted a rearing experiment to test the hypothesis that increment formation is daily and that the otolith continues to grow during eel metamorphosis. We marked the otoliths of wild-caught *Myrophis punctatus* leptocephali and reared these fish through metamorphosis. Metamorphosis was characterized by a decreasing standard length, pre-anal length, and body depth accompanied by an increase in pigmentation and a change in behavior. Increment formation was daily or near-daily through metamorphosis, and the otolith continued to grow during metamorphosis. Thus, the basic tenets of otolith application apply to eel metamorphosis, and non-daily ring deposition and resorption should not be used as explanations for otolith characteristics of eels (e.g., back-calculated hatch dates) unless demonstrated experimentally.

Résumé : Des études récentes sur la métamorphose des anguilles ont été l'occasion de mettre en doute certaines prémisses des analyses basées sur les otolithes. Concrètement, des chercheurs ont allégué que la formation des couches de croissance n'est pas un phénomène journalier et qu'une partie du matériel des otolithes peut être résorbé durant la métamorphose. Nous avons mis au point une expérience d'élevage afin de vérifier l'hypothèse selon laquelle la formation des couches est un phénomène journalier et que les otolithes continuent à croître durant la métamorphose des anguilles. Nous avons marqué les otolithes de leptocéphales de *Myrophis punctatus* capturés en nature et nous avons élevé les poissons jusqu'à la métamorphose. La métamorphose se caractérise par une réduction de la longueur standard, de la longueur pré-anale et de la profondeur du corps, ainsi que par une augmentation de la pigmentation et un changement de comportement. Durant la métamorphose, l'addition de couches de croissance se fait sur une base journalière ou quasi-journalière et les otolithes continuent de croître. Ainsi, les prémisses de base de l'utilisation des otolithes s'appliquent à la métamorphose des anguilles; on ne doit donc pas invoquer la déposition non journalière des anneaux ni la résorption pour expliquer les caractéristiques des otolithes des anguilles (par ex., dans le rétro-calcul des dates d'éclosion) à moins de posséder des preuves expérimentales.

[Traduit par la Rédaction]

Introduction

The analysis of otolith microstructure and chemistry has led to many major advances in fish ecology. Otolith-derived ages have provided time scales for the duration of the larval stage (Victor 1986; Wellington and Victor 1989). Otolith size as a proxy for fish size has been used to examine size-selective mortality (Meekan and Fortier 1996; Hare and Cowen 1997; Vigliola and Meekan 2002). Growth and mortality rates based on otolith ages have contributed to understanding the processes that affect larval and juvenile fish survival (Crecco and Savoy 1987; Rutherford and Houde 1995). Patterns in spawning and settlement based on otolith-derived ages have been used to evaluate links between reproduction and recruitment (Robertson et al. 1999). Otolith chemistry has yielded new insights into the stock structure of species (Thorrold et al. 2001) and the environmental histories of individuals (Secor et al. 2001; Tsukamoto and Arai 2001).

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The application of otolith microstructure and chemical analyses to the study of fish ecology has five central tenets: (*i*) otolith growth increments form at a constant and known rate, typically daily or yearly; (*ii*) otolith growth is proportional to somatic growth; (*iii*) specific patterns in otolith microstructure form at specific life history transitions; (*iv*) otolith material is inert and not reworked after deposition; and (*v*) otoliths incorporate elements in proportion to their availability in the environment. The preceding tenets must hold for most or all individuals in a group or species for results to have applicability beyond the individuals examined in a particular study.

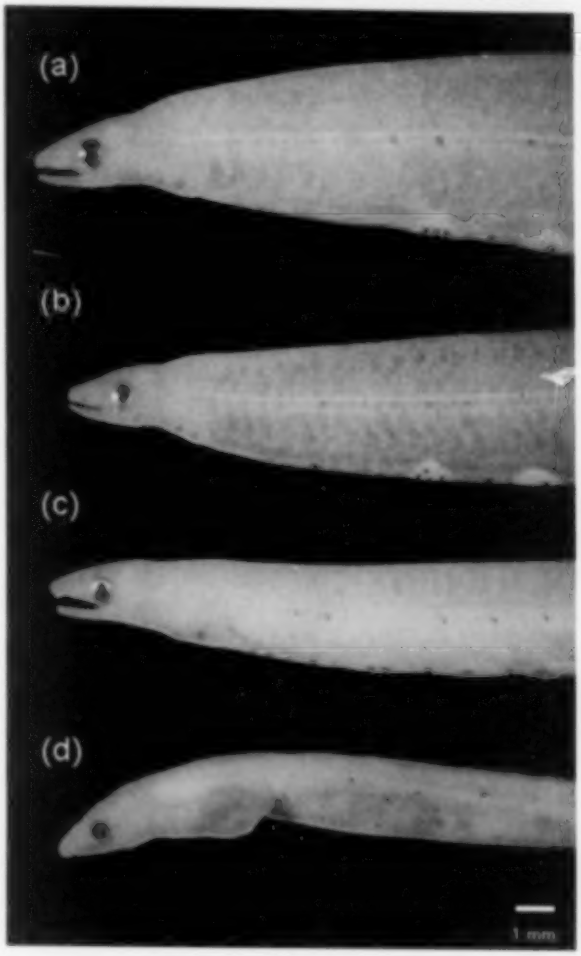
Although these tenets are supported by a large body of experimental and observational evidence (see reviews by Campana and Neilson 1985; Wilson and McCormick 1999; Campana and Thorrold 2001), there are some compelling exceptions. Otolith increment formation is not always daily (e.g., Geffen 1982). The proportionality between otolith and somatic growth is stage-specific for some species (e.g., Hare and Cowen 1995). Settlement marks do not always form on the otoliths of all individuals (e.g., Fowler 1989). The incorporation of some elements into the otolith depends on temperature and salinity, as well as the elemental concentration in seawater (Bath et al. 2000; Martin et al. 2004). Further, elements from water and food must cross several biological membranes to be incorporated into otoliths, and the kinetics of this passage remain largely unresolved (Campana 1999). However, in most instances, these violations are species-, stage-, or case-specific, and although serious, the impact on analyses can be minimized by validation and careful application.

A number of studies have used otoliths to investigate the ecology of eels (e.g., Lecomte-Finiger 1992; Wang and Tzeng 1998; Arai et al. 2000*a*), yet three recent studies have suggested that the basic tenets of otolith application to fish ecology may not apply to eels in the genus *Anguilla* during metamorphosis. Specifically, in a study of *Anguilla anguilla*, Antunes and Tesch (1997) questioned whether increments are deposited in the portion of the otolith corresponding to the period of metamorphosis from leptocephalus to glass eel — the eel equivalent of the larval–juvenile transition. McCleave et al. (1998) questioned the assumption that increment formation is daily in *A. anguilla* leptocephali owing to the lack of species-specific validation studies, uncertain mode of nutrition, and low metabolic rate. Finally, Cieri and McCleave (2000) suggested that otolith material might be resorped during metamorphosis in *Anguilla rostrata*. Cieri and McCleave (2000) noted that eels might absorb their large teeth during metamorphosis (Hulet and Robins 1989), potentially indicating a need for stored calcium. Based on these ideas, Cieri and McCleave (2000) postulated that this calcium in the otolith may be required to complete metamorphosis, and thus, portions of the otolith may be resorped. These hypotheses have not been tested experimentally, but evoke a breakdown of the tenets of otolith application during eel metamorphosis. The question arises: are *A. rostrata* and *A. anguilla* special cases, or are the central tenets of otolith application violated during the metamorphosis of Anguilliformes generally?

Here, we use *Myrophis punctatus* (Anguilliformes, Ophichthidae) as a model species for examining the tenets of otolith application during the metamorphosis of eels. Metamorphosis of *M. punctatus* from leptocephalus to glass eel is similar to metamorphosis of most eel species; the body shape changes from laterally compressed to round, total length decreases then increases, and prominent teeth disappear (e.g., Smith 1989; Bell et al. 2003). Further, *M. punctatus* leptocephali are abundant and can be collected as they enter estuaries (Warlen and Burke 1990), providing a ready supply of specimens for laboratory and field studies.

Our specific objectives were threefold: (*i*) to determine if otolith increments are deposited daily through metamorphosis of *M. punctatus*, (*ii*) to determine if there is resorption of otolith material during metamorphosis, and (*iii*) to evaluate the relation between otolith size and fish size during metamorphosis, when individuals are decreasing in length. We captured leptocephali, marked their otoliths with alizarin

Fig. 1. Stages of *Myrophis punctatus* examined in this study: (*a*) leptocephalus — 78.2 mm total length (TL), 32.7 mm pre-anal length (PAL), 8.4 mm body depth (BD); (*b*) metamorphic — 62.5 mm TL, 27.8 mm PAL, 5.2 mm BD; (*c*) metamorphic — 59.6 mm TL, 23.6 mm PAL, 2.9 mm BD; (*d*) glass eel — 53.6 mm TL, 21.3 mm PAL, 1.9 mm BD.



complexone, and reared them through metamorphosis. Marked otoliths from reared fish were then used to evaluate three of the tenets of otolith application to fish ecology.

Materials and methods

Capture and maintenance

Myrophis punctatus leptocephali (Fig. 1), late euryodontic and early metamorphic stages (Leiby 1979), were captured on two nights: 7 February 2002 from 0300 to 0430 (approximately 80 leptocephali, catch denoted as Series 1); and 20 February 2002 from 0100 to 0300 (approximately 70 leptocephali, catch denoted as Series 2). Fish were captured during flood tide using a 2 m^2 surface net near Pivers Island, North Carolina (see Warlen 1994). A live box was used to keep captured animals in good health during collection (Hettler 1979). Leptocephali were immediately transferred to two 550 L flow-through holding tanks (one for each series) with incoming seawater at ambient temperatures and maintained there until 14 March 2002 (Series 1) and 13 March 2002 (Series 2). Ambient water temperature during the experiments fluctuated from 14.1 to 15.1 °C. Leptocephali were not fed, but it is possible that some small organisms, which passed through the seawater intake filtering system, were available as prey.

Otolith marking

Alizarin complexone was used to produce a permanent, readable mark on the otoliths (Tsukamoto 1988; Ahrenholz et al. 1995). Series 1 fish were placed in 40 L tanks containing 200 $mg \cdot L^{-1}$ alizarin complexone solution in seawater for 7 h on 9 February 2002. Although the leptocephali swam vigorously after being returned to the holding tank, there was some mortality overnight (about 10%). The same procedure was followed for Series 2 fish on 22 February 2002.

Morphometrics

Samples of 5–7 *M. punctatus* were removed from the holding tanks at 4- to 5-day intervals. Individuals were immobilized with tricaine methanesulfonate (MS-222) and measured alive. Morphometric measurements of body proportions were based on Bell et al. (2003), except that body depth was measured at the anus rather than the maximum depth. Measurements were standard length (SL, tip of snout to end of notochord), total length (TL, tip of snout to end of caudal fin), body depth (BD, at the anus), and pre-anal length (PAL, tip of snout to anus). Measurements were made to the nearest 0.1 mm; an eyepiece micrometer was used to measure BD and PAL, and a Vernier caliper was used to measure SL and TL. Fish were then preserved in 95% ethanol and measured again after a period of 1 year. Comparison of live with preserved specimens showed that SL decreased by 10.3%, PAL decreased by 9.5%, and BD decreased by 17.5%. Data were analyzed and presented here as live measurements.

Otolith analysis

Sagittal otoliths from measured specimens were removed, and otoliths were processed according to Secor et al. (1991). First, otoliths were embedded in EmBed 812, an epoxy resin. Then a thin transverse section was cut using an Isomet low speed saw with two blades. One surface of the section was polished using a CrystalMaster polishing machine with 25 μm aluminum grit and fine-polished using a nylon micropolishing cloth with 0.3 μm Alpha Alumina powder. Polishing was conducted until the core was clearly visible and increments discernible. An optical imaging system (video camera attached to a compound microscope and connected to a framegrabber board in a personal computer running Optimas 6.1) was used to measure the distance from the core to the alizarin complexone mark and from the mark to the edge of the otolith. All measurements were made along the longest axis of the otolith. The location of the alizarin complexone mark was determined using an ultraviolet filter

Fig. 2. Mean changes in morphometric characters during metamorphosis of *Myrophis punctatus* leptocephali held in flow-through saltwater tanks: (*a*) standard length, (*b*) pre-anal length, and (*c*) body depth. Error bars around mean values are standard errors. Fish in Series 1 (captured 7 February 2002, *n* = 30) are indicated by solid diamonds; fish in Series 2 (captured 20 February 2002, *n* = 20) are indicated by open circles.

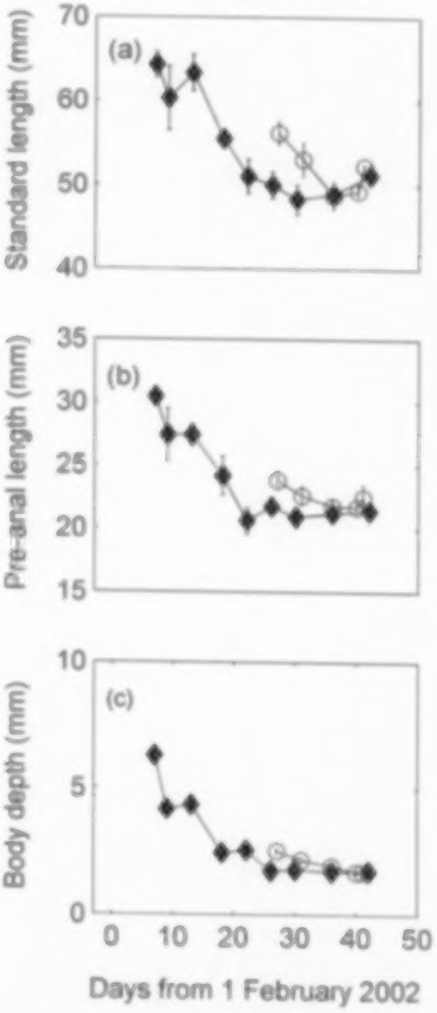
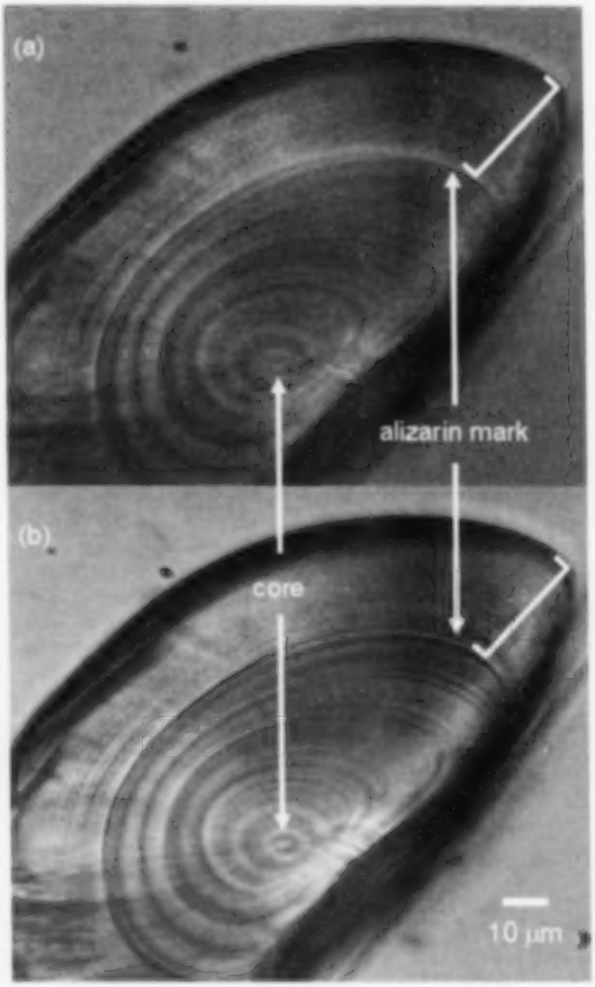
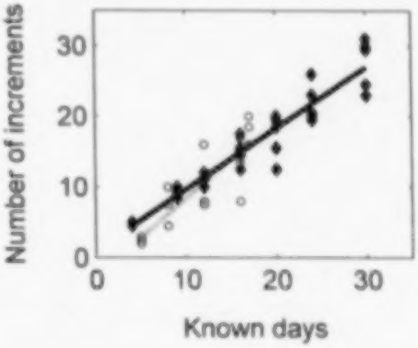


Fig. 3. Transverse section of *Myrophis punctatus* sagittae. (*a*) Image is taken with a combination of ultraviolet and visible light. Alizarin complexone mark is evident as a dark band. (*b*) Image is taken with visible light only. Alizarin complexone mark is evident as a dark band. There are clear increments after the mark, and the region of postmark otolith growth is indicated by a bar. However, one focal plane does not allow clear enumeration of all the postmark increments. The otolith core is also indicated.



(dichroic mirror, 400 nm; excitation filter, 300–380 nm; barrier filter, 420 nm) and green filter (dichroic mirror, 580 nm; excitation filter, 510–560 nm; barrier filter, 590 nm). Presumed daily increments were then counted between the alizarin complexone mark and the edge by two of the authors independently. The average coefficient of variation between the two readers was 6.5%, and the average absolute difference between increment counts was 1.12 increments. Thus, we have confidence in the increment counts presented here. The number of increments was estimated as the mean of the two readers' counts.

Fig. 4. Number of otolith increments relative to days since otolith marking for *Myrophis punctatus* reared through metamorphosis from the leptocephalus to glass eel stage. Otoliths were marked with alizarin complexone, and increment counts were made from the alizarin mark to the edge (see Fig. 3). Fish in Series 1 (captured 7 February 2002) are indicated by solid diamonds; fish in Series 2 (captured 20 February 2002) are indicated by open circles. Linear regressions of increment number on known days are indicated as solid (Series 1) and broken lines (Series 2), although the broken line is largely hidden by solid line. Regression statistics are provided in Table 1.



The three study objectives were then addressed in order. (*i*) Daily increment formation was examined using linear regression of the mean number of increments and known elapsed time from marking to collection. The hypothesis that the regression slopes differed from 1 was tested for each series and for both series combined. (*ii*) Continued otolith growth during metamorphosis was evaluated using linear regression of otolith radius from the alizarin complexone mark to the edge of the otolith and known elapsed time from marking to sampling date. The hypothesis that the regression slopes were greater than 0 was tested for each series and for both series combined. (*iii*) The otolith radius – fish length relation was examined using linear regression. Thorrold and Hare (2002) pointed out that a positive otolith size – fish size relation can exist even if otolith growth and somatic growth are negatively related, simply because both traits are increasing over time (i.e., both are growing). The approach of Hare and Cowen (1995) was used to estimate the relation between otolith growth and body growth. Briefly, the residuals of the length-on-age relation and the otolith size-on-age relation are compared. A positive relation between the residuals indicates that body growth and otolith growth are positively related; a fast-growing fish is large for a given age and has a large otolith for that age, and a slow-growing fish is small for a given age and has a small otolith for that age. A negative relation between the residuals indicates that body growth and otolith growth are negatively related.

Results

Morphology

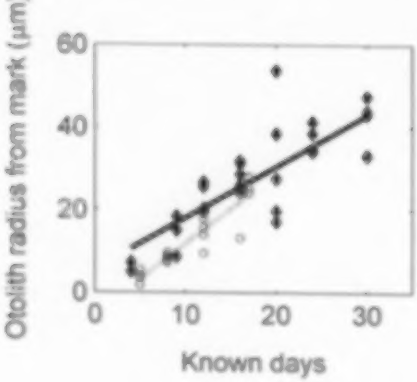
The three stages of *Myrophis punctatus* examined in this study were the late euryodontic leptocephalus (with prominent teeth), the metamorphic stage, and the glass eel stage (Fig. 1). Leptocephali swam throughout the water column (0.5 m deep) within the holding tank. Within the first 3 weeks of capture, leptocephali of *M. punctatus* started to

Table 1. Parameters and statistics for linear regression models of counted increments and known days.

Series	Regression statistics	Slope (H_0: $b = 1$)	y intercept (H_0: $a = 0$)
1	$r^2 = 0.91$, $F_{[30,1]} = 290.85$, $p < 0.001$	$b = 0.87$ ($t_{[30]} = 2.65$, $p < 0.05$)	$a = 1.04$ ($t_{[30]} = 1.07$, $p > 0.05$)
2	$r^2 = 0.78$, $F_{[18,1]} = 62.67$, $p < 0.001$	$b = 1.12$ ($t_{[18]} = 0.86$, $p > 0.05$)	$a = -2.76$ ($t_{[18]} = 1.69$, $p > 0.05$)
1 and 2	$r^2 = 0.89$, $F_{[50,1]} = 393.69$, $p < 0.001$	$b = 0.93$ ($t_{[50]} = 1.42$, $p > 0.05$)	$a = -0.39$ ($t_{[50]} = 0.50$, $p > 0.05$)

Note: Model was $I = a + b \times D$, where I is counted increments, D is known days, and a and b are the regression parameters. Regression statistics, parameters, and results of hypothesis tests are provided.

Fig. 5. Growth of the sagittal otolith of *Myrophis punctatus* during metamorphosis from the leptocephalus to glass eel stage. Otolith growth was measured from the alizarin complexone mark to the edge (see Fig. 3). Fish in Series 1 (captured 7 February 2002) are indicated by solid diamonds; fish in Series 2 (captured 20 February 2002) are indicated by open circles. Linear regressions of otolith radius on known days are indicated as solid (Series 1) and broken lines (Series 2). Regression statistics are provided in Table 2.



show changes in body proportions. SLs and PALs declined for about 25 days from the first date and then remained constant or increased slightly for the remainder of the experiment. SL decreased from an average of 70 mm to 48 mm, then increased gradually to 52 mm (Fig. 2*a*). PAL decreased from an average of 32 mm to 21 mm, then increased slightly to 23 mm (Fig. 2*b*). BD also decreased during the experiment from an average of 6.4 mm to 1.7 mm (Fig. 2*c*). After approximately 20 days, fish became associated with the bottom of the tanks. The gross morphology, morphometric data, and behavioral observations indicated that fish underwent metamorphosis while in captivity. Series 2 fish underwent similar morphometric changes to Series 1 fish, indicating that they went through similar developmental states with similar timing even though they were captured later in development than Series 1 fish.

Otolith characteristics

Under ultraviolet light, the alizarin complexone mark was clear as a red band in all but two fish, providing unquestionable evidence of the initiation of the experiments (Fig. 3*a*). For most individuals, the alizarin complexone mark also was visible with light microscopy, and in all individuals, there were clear increments between the mark and the edge of the otolith (Fig. 3*b*).

The number of increments counted from the mark to the edge was closely related to the known number of elapsed days (Fig. 4). The regression models between known age and counted increments were significant ($p < 0.001$; Table 1). The estimated slope for Series 1 (0.87 increments·day^{-1}) was significantly different than 1, while the estimated slopes for Series 2 (1.12 increments·day^{-1}) and both series combined (0.93 increments·day^{-1}) were not significantly different than 1 (Table 1). The *y* intercepts for all three regression models were not significantly different than zero (Table 1). These results indicated that increment formation was near-daily or daily during metamorphosis of *M. punctatus*.

The otoliths of both series of *M. punctatus* continued to grow during metamorphosis from leptocephalus to glass eel stage (Fig. 5). The mean otolith distance from mark to outer edge increased from 5 to 40 µm in Series 1 fish over 30 days and from 5 to 25 µm in Series 2 fish over 15 days. The otoliths grew about 1.4 µm·day^{-1}, and the slopes of the regressions of otolith radius on age were significantly greater than zero for fish from both Series (Table 2).

As expected from decreasing body sizes (Fig. 2*a*) and growing otoliths (Fig. 5), the otolith radius – standard length relationship was negative (Fig. 6*a*). The slope of the regressions for Series 1 and for both series combined were significantly less than zero, while the slope of the regression for Series 2 was not (Table 3). The regression slopes of the length-on-age residuals and otolith radius-on-age residuals were negative for the two series and for both series combined, but none were significantly different than zero (Table 4). Thus, otolith growth and somatic growth were not related during metamorphosis of *M. punctatus*.

Discussion

Eel metamorphosis from leptocephali to glass eel is extreme (Smith 1989). Morphometric changes are very pronounced during metamorphosis of *Conger myriaster* and *Conger oceanicus*, with decreases in total length and body depth (Lee and Byun 1996; Bell et al. 2003). The anus often moves forward, shortening the PAL (Smith 1989; Bell et al. 2003). Larval teeth are lost, possibly through resorption (Hulet 1978; Hulet and Robins 1989). Pigmentation changes dramatically from the lightly pigmented leptocephali, to partially pigmented glass eels, to fully pigmented elvers (Haro and Kreuger 1988; Bell et al. 2003). In general, the metamorphic stage can be defined from the maximum leptocephalus size to the minimum size of the benthic glass eel stage (Bell et al. 2003), and our samples contained mainly leptocephali slightly under the maximum length (70 vs. 80 mm SL). Based on these descriptions and definition of eel metamorphosis, we are confident that we reared

Table 2. Parameters and statistics for linear regression models of otolith radius from mark to edge and counted increments.

Series	Regression statistics	Slope (H_0: $b = 0$)	y intercept (H_0: $a = 0$)
1	$r^2 = 0.67$, $F_{[29,1]} = 57.70$, $p < 0.001$	$b = 1.25$ ($t_{[29]} = 7.60$, $p < 0.001$)	$a = 5.58$ ($t_{[29]} = 1.75$, $p > 0.05$)
2	$r^2 = 0.88$, $F_{[18,1]} = 131.37$, $p < 0.001$	$b = 1.71$ ($t_{[18]} = 11.46$, $p < 0.001$)	$a = -5.31$ ($t_{[18]} = 3.10$, $p < 0.05$)
1 and 2	$r^2 = 0.77$, $F_{[49,1]} = 162.84$, $p < 0.001$	$b = 1.50$ ($t_{[49]} = 12.76$, $p < 0.001$)	$a = -0.53$ ($t_{[49]} = -0.27$, $p > 0.05$)

Note: Model was $\mathrm{OR}_{\mathrm{me}} = a + b \times I$, where $\mathrm{OR}_{\mathrm{me}}$ is the otolith radius from mark to edge, I is counted increments, and a and b are the regression parameters. Regression statistics, parameters, and results of hypothesis tests are provided.

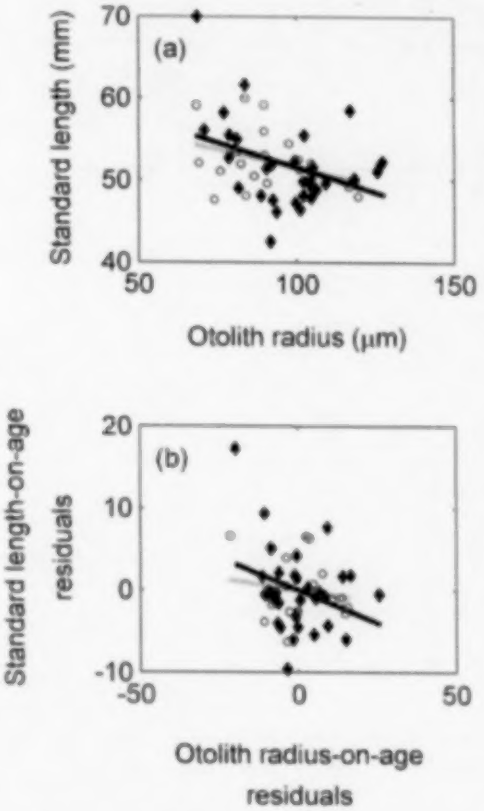


Fig. 6. (*a*) Relation between body size and otolith size during metamorphosis from the leptocephalus to glass eel stage in *Myrophis punctatus*. Linear regressions of standard length on otolith radius are indicated as solid (Series 1) and broken (Series 2) lines. Regression statistics are provided in Table 3. (*b*) Relation between estimates of body growth and otolith growth during metamorphosis from leptocephali to glass eels in *M. punctatus*. Body growth was estimated as the residuals of length-on-age (fish with large, positive residuals were faster growing). Otolith growth was estimated as the residuals of otolith radius-on-age (otoliths with large, positive residuals were faster growing). Linear regressions of length-on-age residuals on the otolith size-on-age residuals are indicated as solid (Series 1) and dashed (Series 2) lines. Fish in Series 1 (captured 7 February 2002) are indicated by solid diamonds; fish in Series 2 (captured 20 February 2002) are indicated by open circles. Regression statistics are provided in Table 4.

M. punctatus from the euryodontic leptocephalus stage, through metamorphosis, into the glass eel stage.

Increment formation was found to be daily or near-daily through metamorphosis from the leptocephalus to glass eel stage in *M. punctatus*. Daily increment formation has been documented in glass eel and elver stages (e.g., Tsukamoto 1989; Martin 1995; Cieri and McCleave 2001), leptocephalus stage (Shinoda et al. 2004), and pre-leptocephalus stage (Umezawa et al. 1989) for several species of eels. Daily increment formation also has been confirmed through metamorphosis of two *Megalops* species (Tzeng et al. 1998; Zerbi et al. 2001), which are in the order Elopiformes and have leptocephalus larvae similar to fishes in the order Anguilliformes (Miller and Tsukamoto 2004). Thus, the body of evidence is similar for eels as for other fishes: daily increment formation occurs in early life stages during normal conditions, and based on this body of evidence, we conclude that the a priori assumption of daily otolith formation in eel early life stages should be considered valid until rejected by direct laboratory or field evidence.

Myrophis punctatus otoliths grew during metamorphosis even though individuals were decreasing in body length. Using field-collected specimens, Lee and Byun (1996) inferred that otolith growth continued during metamorphosis of *Conger myriaster*. Otolith growth also continued during the metamorphosis of two elopiform fishes, which also shrink during metamorphosis (Tzeng et al. 1998; Zerbi et al. 2001). Otolith growth continues through the metamorphosis of most other fish species as well (e.g., amphidromous gobiids, Shen and Tzeng 2002; clupeids, Fey 2000; labrids, Searcy and Sponaugle 2000; myctophids, Linkowski et al. 1993; pleuronectids, Sogard 1991; pomatomids, Hare and Cowen 1994; sciaenids, Fey et al. 2005), and thus, otolith resorption is not a common trait of anguilliform metamorphosis, not a common trait of elopomorph metamorphosis, nor a common trait of fish metamorphosis generally, even though dramatic morphological and physiological changes take place. We conclude that the a priori assumption that otolith growth continues during metamorphosis should be considered valid until rejected by direct laboratory or field evidence.

Fish metamorphosis is often accompanied by marks or checks on otoliths. Secondary primordia form during the larval–juvenile transition in flatfish (*Pseudopleuronectes americanus*) (Sogard 1991) and bluefish (*Pomatomus saltatrix*) (Hare and Cowen 1994), and distinct increment patterns form in otoliths of many reef fish at settlement (Wilson and McCormick 1997; Searcy and Sponaugle 2000). In eels, a check forms in the otolith during metamorphosis (Lecomte-Finiger 1992; Correia et al. 2002, 2004). The application of otolith research to fish ecology would be strengthened by a physiological understanding of the forma-

Table 3. Parameters and statistics for linear regression models of otolith radius and standard length.

Series	Regression statistics	Slope (H_0: $b = 0$)	y intercept (H_0: $a = 0$)
1	$r^2 = 0.14$, $F_{[30,1]} = 4.80$, $p < 0.05$	$b = -0.12$ ($t_{[30]} = 2.19$, $p < 0.05$)	$a = 63.70$ ($t_{[30]} = 11.54$, $p < 0.001$)
2	$r^2 = 0.11$, $F_{[18,1]} = 2.22$, $p > 0.05$	$b = -0.09$ ($t_{[18]} = 1.49$, $p > 0.05$)	$a = 60.32$ ($t_{[18]} = 11.21$, $p < 0.001$)
1 and 2	$r^2 = 0.13$, $F_{[50,1]} = 7.58$, $p < 0.01$	$b = -0.11$ ($t_{[50]} = 2.75$, $p < 0.01$)	$a = 62.34$ ($t_{[50]} = 16.39$, $p < 0.001$)

Note: Model was OR = $a + b \times$ SL, where OR is otolith radius, SL is standard length, and a and b are the regression parameters. Regression statistics, parameters, and results of hypothesis tests are provided.

Table 4. Parameters and statistics for linear regression models of the residuals of otolith radius-on-age and standard length-on-age.

Series	Regression statistics	Slope (H_0: $b = 0$)	y intercept (H_0: $a = 0$)
1	$r^2 = 0.09$, $F_{[29,1]} = 2.91$, $p > 0.05$	$b = -0.16$ ($t_{[29]} = 1.71$, $p > 0.05$)	$a = 0$ ($t_{[29]} = 0$, $p > 0.05$)
2	$r^2 = 0.02$, $F_{[18,1]} = 0.44$, $p > 0.05$	$b = -0.06$ ($t_{[18]} = 0.66$, $p > 0.05$)	$a = 0$ ($t_{[18]} = 0$, $p > 0.05$)
1 and 2	$r^2 = 0.07$, $F_{[49,1]} = 3.74$, $p > 0.05$	$b = -0.11$ ($t_{[49]} = 1.94$, $p > 0.05$)	$a = 0$ ($t_{[49]} = 0$, $p > 0.05$)

Note: Model was $\text{RES}_{\text{OR-A}} = a + b \times \text{RES}_{\text{SL-A}}$, where $\text{RES}_{\text{OR-A}}$ and $\text{RES}_{\text{SL-A}}$ are the residuals of otolith radius-on-age and standard length-on-age, respectively, and a and b are the regression parameters. Regression statistics, parameters, and results of hypothesis tests are provided.

tion of the marks and checks associated with the larval–juvenile transition (Wilson and McCormick 1997, 1999; Thorrold and Hare 2002). For many fish species, enumerating increments through these marks and checks is challenging, and much of the uncertainty regarding the application of otoliths to the study of eel ecology arises during the interpretation of the opaque zone (Antunes and Tesch 1997; Cieri and McCleave 2000; Correia et al. 2002). In *M. punctatus*, metamorphosis seems to be indicated by a check, not an opaque zone (P.M. Powles, unpublished data), therefore interpreting otolith microstructure may have been easier than in species that form an opaque zone during metamorphosis (e.g., *Anguilla* spp.). Correia et al. (2004) summarized that this opaque zone could result from very small daily growth increments (sensu Campana et al. 1987), otolith resorption (sensu Cieri and McCleave 2000), or poor otolith preparation (sensu Arai et al. 2000*b*). Continued otolith growth during metamorphosis has been demonstrated experimentally here for an anguilliform (*M. punctatus*) and by Tzeng et al. (1998) and Zerbi et al. (2001) for elopiform fishes, indicating that the metamorphic zone is not caused by otolith resorption. Further, a number of studies have reported ages for glass and elver stage eels (e.g., Wang and Tzeng 1998; Marui et al. 2001; Powles and Warlen 2002), indicating that with careful otolith preparation and proper training of readers, counting increments in this zone is possible.

A third tenet of otolith application examined in this study — otolith growth is proportional to somatic growth — is clearly violated during the metamorphosis of *M. punctatus*. During the leptocephalus stage, the otolith grows and body length increases. During metamorphosis, body length decreases and the otolith continues to grow. This negative relation between growth in length and growth in otolith size has also been documented in the metamorphic stages of *Conger myriaster* (Lee and Byun 1996) and two species of *Megalops* (Tzeng et al. 1998; Zerbi et al. 2001) and is likely a general characteristic of elopomorph metamorphosis. The problems with applying size back-calculation techniques in species that have stage-specific relations between otolith and somatic growth have been discussed in Hare and Cowen (1995) and Thorrold and Hare (2002), but elopomorph fishes present an extreme example. Size back-calculation should not be attempted in the early stages of elopomorph fishes until otolith size – fish size relations and otolith growth – fish growth relations are determined over the entire early life history of an eel species and stage-specific back-calculation techniques are developed.

Recent studies have questioned whether the tenets of otolith application apply to the early life history of eels, specifically *A. anguilla* and *A. rostrata*. Antunes and Tesch (1997) and McCleave et al. (1998) questioned whether increment formation is daily during metamorphosis, and Cieri and McCleave (2000) proposed that otolith material might be resorped during metamorphosis. If these hypotheses are valid, then otoliths have limited application to the study of eel ecology, particularly during the metamorphic period. Further, otolith resorption in eels raises the specter of otolith resorption in other species, which violates the basic tenet of otolith chemistry — the material in otoliths is biologically inert. In one regard, the questions of Antunes and Tesch (1997), McCleave et al. (1998), and Cieri and McCleave (2000) were raised because hatch date distributions based on otolith ages were broader in time (e.g., Lecomte-Finiger 1992; Wang and Tzeng 1998; Powles and Warlen 2002) than spawning dates estimated from the occurrence of small leptocephali in the Sargasso Sea (reviewed by McCleave et al. 1998). The validation of daily otolith increment formation and continued otolith growth during metamorphosis of *M. punctatus* demonstrate that these tenets of otolith application are not violated during the metamorphosis of one eel species (see also Lee and Byun 1996). Further, Tzeng et al. (1998) and Zerbi et al. (2001) indicated that these tenets of otolith application hold for the metamorphic stage of two species of Elopiformes. Thus, these tenets hold for all species of elopomorph fishes where they have been examined directly. We conclude that without experimental demonstration, otolith resorption and non-daily increment formation should not be used as explanations for the otolith characteristics of eels.

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Physiology of individual late-run Fraser River sockeye salmon (*Oncorhynchus nerka*) sampled in the ocean correlates with fate during spawning migration

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Abstract: Beginning in 1995, segments of the late-run sockeye salmon (*Oncorhynchus nerka*) stocks from the Fraser River, British Columbia, have initiated upriver spawning migration up to 6 weeks earlier than historical records; and those fish have experienced high rates of en route mortality. We examined the correlations between physiological and energetic status prior to river entry with subsequent migratory performance of individual salmon using telemetry and noninvasive biopsies for Adams–Thompson–Shuswap (Adams) and Weaver–Harrison (W–H) stocks. Salmon that failed to reach the river were characterized by a tendency to have elevated levels of chronic and acute stress indicators. For one stock of fish (i.e., Adams) that entered the river, those that died before reaching spawning grounds were individuals with low gross somatic energy. Furthermore, females tended to have elevated plasma estradiol levels. When contrasting fish with different behaviours and fates, fish that did not hold in the estuary and subsequently died tended to have less energy than fish that held and reached spawning areas. Females from the former group also had higher 11-ketotestosterone and estradiol levels relative to those from the later group. These data suggest that differences in physiological and energetic status may be associated with high en route mortality in late-run sockeye salmon.

Résumé : Depuis 1995, des portions des stocks à migration tardive de saumons rouges (*Oncorhynchus nerka*) du Fraser, Colombie-Britannique, commencent leur migration de reproduction vers l'amont jusqu'à six semaines avant la période normale du passé et elles subissent de forts taux de mortalité durant le trajet. Nous examinons les corrélations entre les statuts physiologique et énergétique avant l'entrée en rivière et la performance subséquente de la migration chez des saumons individuels des stocks Adams–Thompson–Shuswap (Adams) et Weaver–Harrison (W–H) à l'aide de la télémétrie et de biopsies non invasives. Les saumons qui n'atteignent pas la rivière ont tendance à avoir des niveaux élevés d'indicateurs de stress chronique et aigu. Chez l'un des stocks (c.-à-d., Adams) qui a pénétré dans la rivière, les poissons qui sont morts avant d'atteindre les sites de fraye étaient des individus possédant une faible énergie somatique brute. De plus, les femelles avaient tendance à avoir des concentrations plasmatiques élevées d'oestradiol. En comparant des poissons ayant des comportements et des sorts différents, nous trouvons que les poissons qui ne se sont pas maintenus dans l'estuaire et qui sont morts subséquemment avaient tendance à avoir moins d'énergie que les poissons qui se sont maintenus et qui ont atteint les sites de fraye; les femelles du premier groupe avaient aussi des concentrations plus élevées de 11-céto-testostérone et d'oestradiol que celles du second groupe. Ces données indiquent que les statuts physiologique et énergétique peuvent être associés à une forte mortalité durant le trajet chez le saumon rouge.

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Introduction

In the Fraser River, British Columbia (B.C.), there are a number of economically, culturally, and ecologically important sockeye salmon (*Oncorhynchus nerka*) stocks. Therefore, it is not surprising that both fisheries managers and the broader public are concerned when large proportions of upriver-migrating sockeye salmon perish before reaching their spawning grounds. Mortality during spawning migration is a natural and expected outcome for a segment of any population and serves as a major selective force (Dingle 1980). Indeed, historic records of en route mortality for sockeye salmon are typically near 10%, with much higher levels observed in years when environmental conditions make migration more difficult for fish (Gilhousen 1990; Macdonald 2000). To date, a number of environmental conditions such as elevated levels of water temperature, suspended sediment, and water discharge are known to make migration more difficult and have been associated with in-river mortality (Macdonald et al. 2000). When these conditions collectively exceed the tolerance and (or) capabilities of the fish, en route mortality can occur (Rand and Hinch 1998; Hinch and Bratty 2000).

Migration is regarded as one of the most energetically demanding and physiologically challenging phases of a fish's life history. It represents one of the most complex interplays between behaviour and physiology (McKeown 1984; Lucas and Baras 2001; Hinch et al. 2005). Individual migrants can vary in their physiological (Lee et al. 2003; Shrimpton et al. 2005) and energetic (Hinch and Rand 1998; Kinnison et al. 2001) status, perhaps because of environmental influences and also genetic disposition. Despite the large body of research evaluating salmonid migrations, we know little about what differentiates a successful migrant from one that dies while en route to the spawning grounds (Lucas and Baras 2001; Hinch et al. 2005; Cooke et al. 2006). Such information is particularly important in years when mortality rates are quite high.

When fisheries managers document high levels of migration mortality for several sequential years that cannot be explained solely by in-river environmental conditions, uncertainty puts stocks at risk of extinction and generates conflict among different fishing sectors. In recent years, the late-run sockeye salmon stocks in the Fraser River have been experiencing a pattern of persistently high levels of mortality during spawning migrations, as well as alterations in their migration behaviour (Cooke et al. 2004*b*; Lapointe et al. 2004). These late-run sockeye salmon stocks represent one of four stock complexes in the Fraser River watershed distinguished by the timing of freshwater entry and the location of spawning (Killick 1955; Woodey 1987). They arrive in August near the mouth of the Fraser River in the Strait of Georgia (Fig. 1), where they normally remain for 3–6 weeks prior to initiating upriver migration. However, since 1995, segments of the population have initiated upriver migration up to 6 weeks earlier and therefore have reduced or eliminated their historic estuarine delay behaviour (Cooke et al. 2004*b*; Lapointe et al. 2004). Early migration does not confer an earlier spawning date, but instead is associated with high mortality rates, which in some years exceeds 90% for several stocks (Cooke et al. 2004*b*; Lapointe et al. 2004).

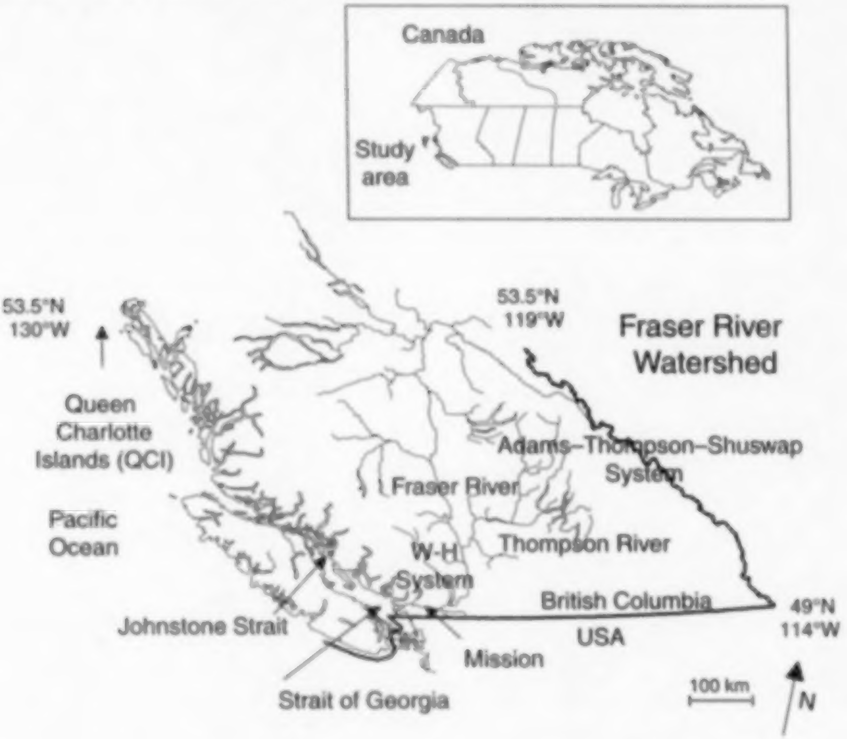
The objective of the present study was to evaluate the correlations between physiological and energetic status prior to river entry with their subsequent migratory performance (failure or success) in an attempt to understand this high mortality phenomenon. We tested the hypothesis that physiological and energetic status varies with migration fate. We predicted that failed migrants may exhibit elevated levels of stress indicators, low somatic energy, and advanced levels of reproductive and osmoregulatory preparedness in the marine environment. These predictions are based on a number of proposed behavioural and mortality mechanisms discussed in Cooke et al. (2004*b*). The majority of these predictions are intuitive aside from the one dealing with osmoregulatory preparedness. Our rationale for that prediction is that fish with advanced osmoregulatory preparedness may initiate upriver mortality prematurely and thus face higher water temperatures en route (Wagner et al. 2005). To test our hypothesis, we contrasted successful and unsuccessful migrants during (*i*) their coastal migration through to river entry and (*ii*) their upriver migration to terminal spawning grounds. We also contrasted individuals that exhibited different marine delaying behaviours to specifically determine why mortality is higher in fish that do not hold. Our efforts focused on trying to elucidate the potential mechanistic basis for the observed high levels of en route mortality for late-run sockeye salmon, recognizing that causation could only be concluded after subsequent manipulative experiments. Eventually, it is our hope to develop a suite of predictive physiological tools that would aid in the management and conservation of late-run sockeye salmon and other Pacific salmonids. To address our objectives, we intercepted sockeye salmon in the coastal ocean environment as they headed toward the Fraser River estuary where they would begin their upriver migration. Fish were implanted with radio transmitters to follow their subsequent migration behaviour and to determine their fate. These same individuals were also biopsied, which included drawing blood from the caudal vessels, removing some gill filament tips, and quantifying energetic status using a microwave energy meter (Cooke et al. 2005). Radio receiving systems were deployed throughout the Fraser River and to its tributaries over a distance of ~500 km.

Materials and methods

Sampling strategy

The present investigation was part of a larger telemetry study in which sockeye salmon ($N = 559$) were intercepted near the southern end of Johnstone Strait, B.C., Canada (Fig. 1), approximately 215 km from the mouth of the Fraser River (see English et al. 2004). We developed protocols to biopsy a portion ($N = 301$) of these sockeye salmon (Cooke et al. 2005). Fish were sampled without anaesthesia. Anaesthetics currently approved for use in fish should not be ingested by humans and because the fish were released to the ocean to resume their normal migration, the possibility existed that they might be subsequently caught by fishers or other animals and consumed. Our protocols, which were approved by The University of British Columbia Animal Care Committee, were validated in a parallel study, in which three independent assessments were used to demonstrate that it was possible to biopsy and tag sockeye salmon without causing

Fig. 1. Map of study system inset within Canada and the Fraser River Watershed of British Columbia (B.C.). Fish were implanted with transmitters and biosampled in Johnstone Strait, a coastal area where fish begin to encounter estuarine conditions. Late-run sockeye salmon (*Oncorhynchus nerka*) typically delay in the Strait of Georgia for several weeks prior to entering the river. A radio telemetry receiver array was deployed at Mission, B.C., 85 km upriver from the mouth of the Fraser River to monitor entry. This analysis focused on late-run sockeye from the Weaver–Harrison (W–H) or Adams–Thompson–Shuswap stock groups.



deleterious effects to behaviour or survival (Cooke et al. 2005).

Fish were collected using a large purse seine net deployed from a commercial fishing vessel, which also served as the platform for biopsy, radio-tagging, and fish release. Fish were sampled, tagged and released over a 3-week period between 11 August and 28 August 2003 at surface water temperatures of 10–13 °C. Fish were first detected (i.e., arrival in the Fraser River) by two radio telemetry stations approximately 300 km from the release site at Mission, B.C., beyond the tidal boundary and 85 km upstream from the mouth of the river (Fig. 1). We defined an individual fish as successfully completing river entry once it was detected at the Mission telemetry station. Twelve additional telemetry stations were deployed at intervals along the mainstem Fraser and Thompson rivers and appropriate late-run terminal spawning grounds (e.g., Adams–Thompson–Shuswap (hereafter referred to as Adams), total distance of 400 km from Mission; Weaver–Harrison (W–H), total distance of 85 km from Mission; Fig. 1). These receiving stations were equipped with up to three antennas and a data-logging radio receiver (SRX_400, Lotek Engineering Inc., Newmarket, Ontario), as detailed in English et al. (2004). Mobile tracking was also conducted by foot and boat. To encourage reporting of fish harvested by recreational anglers, commercial fishers, and First Nations fishers, we implemented a public awareness campaign and offered a small reward for information and transmitter return. Receivers were also used to scan for transmitters at three of the largest (by volume) fish processing plants in B.C. Reporting compliance was believed to be high (English et al. 2004), but any unreported harvesting would result in an overestimate of our mortality percentages.

Synopsis of biopsy and tagging techniques

Following capture, individual fish were netted from the purse (which remained in the water and was gathered at the side of the vessel) and placed in large flow-through totes on deck. Individuals were then removed from the tote, placed ventral-side-up in a padded V-shaped trough, and provided with a continuous supply of fresh, ambient seawater via a tube placed near the mouth. Fish were manually restrained for less than 3 min, during which time fork length (cm) was measured, tissues were biopsied, and a radio transmitter was inserted. The biopsy procedure involved (*a*) removing a small piece (0.5 g) of the adipose fin for DNA stock identification, (*b*) removing one scale for ageing, (*c*) removing 3 mL of blood from the caudal vessel using a vacutainer syringe (1.5 inch, 21 gauge; Houston 1990) for assessing plasma chemistry, and (*d*) removing <4 mm from the tips of six to eight filaments (0.03 g) from the first gill arch (McCormick 1993) for assessing gill Na^+/K^+ ATPase activity. Gill tissue and centrifuged plasma samples were stored on dry ice for several days until being transferred to a –80 °C freezer, where they were held until analysis. A hand-held microwave energy meter (Distell Fish Fatmeter model 692, Distell Inc., West Lothian, Scotland, UK) was placed on the left side of the fish in two locations to quantify gross somatic energy levels (see Crossin and Hinch 2005). Radio transmitters, which measured 16 mm in diameter and 51 mm in length and weighed 16.1 g in air and 6.2 g in water (MCFT-3A, Lotek Inc., Newmarket, Ontario), were orally inserted into the stomach using a plastic applicator. Fish were returned to the holding tote to recover for <1 h after this procedure. All fish in the tote were released as a group in an attempt to minimize predation by marine mammals.

Assays

The present analysis focused on fish from the two largest late-run sockeye stock groups: the W–H and the Adams stocks (Fig. 1). Stock origin was ascribed to individual fish by a combination of DNA analyses (Beacham et al. 1995, 2004) and the recovery of radio transmitters at spawning grounds. Stock assignment through DNA analysis is a standard technique in fisheries management, and research for Fraser River sockeye salmon and overall has 96% accuracy (T. Beacham, Fisheries and Oceans Canada, Pacific Biological Station, Hammond Bay Road, Nanaimo, B.C., V9R 5K6, personal communication). In our study, we focused on identifying late-run fish and then differentiating them into two primary stock groupings (i.e., W–H and Adams), which are each composed of a number of differentiated populations. Thus, for our purposes DNA accuracy was likely higher than 96%. Indeed, we observed no instances of incongruence between DNA analyses and arrivals at terminal spawning grounds for late-run sockeye supporting that idea. Furthermore, exclusion probabilities were uniformly high for fish that reached spawning grounds and fish that died en route for each of the two late-run stock complexes (*t* tests: W–H, $t = 0.185$, $P = 0.855$, mean ± standard deviation (SD), survivors 0.97 ± 0.09, mortalities 0.98 ± 0.06; Adams, $t = -0.348$, $P = 0.729$, survivors 0.91 ± 0.12, mortalities 0.90 ± 0.12). Of 559 sockeye sampled and released in the larger investigation, 188 fish were identified as late-run. We excluded six fish from other smaller late-run stocks, leaving data for 182 fish. The physiological analysis was restricted to 146 late-run fish, 117 of which had had tissue biopsies and energy measurements, while a further 29 fish had only energy measurements before release. The remaining fish were released with transmitters without being biosampled.

Plasma testosterone, 17β-estradiol, and 11-ketotestosterone levels were measured by radioimmunoassay (McMaster et al. 1992) and used to assign gender. Plasma ion (K^+, Cl^-, Na^+), cortisol, lactate, glucose, and osmolality measurements followed the procedures described by Farrell et al. (2001). Gill tissue Na^+/K^+ ATPase activity was determined with a kinetic assay (McCormick 1993) and expressed as μmol ADP·mg protein^{-1}·h^{-1}. Detailed description of all assays presented here, including the interassay variability and quality control criteria, are provided in Farrell et al. (2001).

Statistical analysis

Multivariate analysis of variance (MANOVA) on $\log_{10}$-transformed data (McGarigal et al. 2000) revealed that stock-specific differences were only apparent for energetic and size information, so we pooled data from both W–H and Adams for all other biological characteristics. Two-sample *t* tests or their nonparametric equivalent (i.e., Mann–Whitney *U* test when data were non-normal) were used to contrast the physiological and energetic status by fate. Fate was assessed during (*i*) the river entry migration phase (i.e., excluding fishery removals, we compared fish that entered the Fraser River versus those that failed to do so) and (*ii*) the in-river migration phase (i.e., of fish that entered the river and were not harvested, we compared those that did not reach terminal spawning grounds in their natal subwatershed with those that were successful). Because each stock complex is composed of multiple populations, we used arrival in the natal subwatershed rather than arrival at actual spawning grounds as a proxy for success. "River entry" fish were those that were detected at the downstream telemetry receiving station at Mission, B.C. Reproductive hormone assays were restricted to fish that entered the river, so statistical analysis was only conducted for the in-river migration phase. For each hormone, sex was treated separately for statistical analysis.

All analyses were conduced using JMP 4.0 (SAS Institute Inc., Cary, North Carolina). Because of multiple comparisons, we conducted simultaneous Bonferroni corrections (Zar 1996). We selected an initial α of 0.10 so that we did not end up with overly conservative α levels after Bonferroni corrections (see Cabin and Mitchell 2000) and to increase statistical power (i.e., reduce type II errors; Peterman 1990). For analyses, we present corrected and uncorrected α levels (see Tables 1, 2, and 3) to enable the reader to perform their own assessment as to which significance criteria to observe (as per Cabin and Mitchell 2000). As a secondary assessment of the role of conducting multiple comparisons, binomial likelihood tests were completed for each analysis to determine if the number of tests that were significant was more than expected by chance ($P = 0.10$). Retrospective power analyses were conducted (*i*) using the observed effect size and variance and (*ii*) using a predetermined effect size (5%) and the observed variance (Thomas 1997). Power analyses were conducted to aid in the interpretation of data and are presented in concert with *P* values in tabular form.

Results

River entry migration phase

Of the 182 late-run sockeye salmon released that avoided the ocean fishery (i.e., 181, one was harvested), 67 (37%) individuals failed to enter the Fraser River. Sockeye salmon that failed to enter the Fraser River exhibited a number of physiological differences relative to those that were successful. Indicators of chronic and acute stress including plasma glucose ($P = 0.076$), plasma lactate ($P < 0.001$), and plasma cortisol ($P = 0.090$) had been higher in fish that failed to enter the river (Table 1). Plasma Na^+ ($P = 0.009$) had been higher in sockeye salmon that entered the river, whereas plasma osmolality ($P = 0.002$) had been higher in fish that did not (Table 1). No other significant differences were noted despite there being reasonable power for most analyses (Table 1).

Table 1. Comparison of biological variables between late-run sockeye salmon (*Oncorhynchus nerka*) that died before entering the Fraser River at Mission, B.C., with those that survived to Mission, B.C.

Variables	Died prior to river entry	N	Survived to river entry	N	Test statistic	P value	Observed power	Effect size power
Nose fork length (cm)								
W–H	60.6±0.5	27	60.9±0.5	31	t, –0.52	0.605	0.144	1.000
Adams	61.0±0.4	40	61.2±0.3	83	t, –0.58	0.559	0.157	1.000
Gross somatic energy ($MJ\cdot kg^{-1}$)								
W–H	8.27±0.21	26	7.85±0.18	27	t, 1.55	0.126	0.458	0.419
Adams	9.22±0.09	37	9.14±0.07	66	t, 0.70	0.483	0.182	0.990
Plasma								
Ions ($mmol\cdot L^{-1}$)								
Na^+	182.5±1.2	48	186.6±0.9	72	t, –2.65	**0.009**	0.839	1.000
K^+	1.26±0.15	48	1.53±0.12	72	t, –1.33	0.186	0.376	0.981
Cl^-	147.4±0.6	46	148.4±0.6	69	t, –1.17	0.245	0.317	1.000
Osmolality ($mosmol\cdot kg^{-1}$)	354.9±2.3	48	345.8±1.8	73	t, 3.14	**0.002**	0.931	1.000
Cortisol ($ng\cdot mL^{-1}$)	562.6±56.3	47	458.2±32.9	73	t, 1.71	*0.090*	0.523	0.129
Lactate ($mmol\cdot L^{-1}$)	11.36±0.59	48	9.01±0.37	73	t, 3.50	**<0.001**	0.967	0.195
Glucose ($mmol\cdot L^{-1}$)	7.46±0.18	48	7.07±0.12	73	t, 1.79	*0.076*	0.554	0.518
Na^+/K^+ ATPase (μmol $ADP\cdot mg$ $protein^{-1}\cdot h^{-1}$)	2.75±0.17	15	2.61±0.12	72	U, 0.50	0.618	0.142	0.168

Note: Fishery losses from the ocean were excluded from analyses. Multiple analysis of variance revealed that stock differences were only significant for energetics and size variables, so for all other analyses we pooled fish from both the Weaver–Harrison (W–H) and Adams–Thompson–Shuswap (Adams) stock groups. All other analyses represent all late-run sockeye that passed Mission. Analyses were conducted using two-sample t tests when data were normal and met the homogeneity of variance assumption. Italicized statistical output indicates significant differences at $\alpha = 0.10$. Because we conducted multiple comparisons, Bonferroni corrections were applied and significant values based on this criterion (i.e., $\alpha = 0.01$) were bolded. A binomial likelihood test revealed that the number of tests that were significant was greater than expected by chance ($P = 0.004$). Retrospective power analyses ($1 - \beta$) are reported in two forms. Observed power was calculated using the observed effect size and variance. Effect size power was calculated using a predetermined effect size of 5% and the observed variance.

Upriver migration phase

Excluding in-river fishery removals ($N = 6$), 108 late-run sockeye salmon passed the lower river telemetry station and initiated upriver migration (Table 1). Of these fish, 39 (36.1% for both stock groups, 36.6% for W–H and 35.9% for Adams) failed to reach their natal spawning ground and were considered en route mortalities. Overall, 69 late-run sockeye (63.9% of fish that entered the river and avoided harvest) were considered successful migrants. Of the 182 late-run sockeye tagged in the Johnstone Strait (excluding the seven harvested fish), 38.1% reached their natal sub-watershed. Fewer physiological variables were associated with upriver fate than with the previous river entry migration phase. Gross somatic energy was lower ($P = 0.078$) in fish that failed to reach spawning grounds from the Adams stock but not for W–H (Table 2). For females, estradiol hormone titres was higher ($P = 0.097$) in fish that died en route relative to successful migrants (Table 2). No other physiological variables differed statistically with fate, although statistical power was generally low for most endocrine and stress indicators (i.e., $1 - \beta < 0.70$), suggesting that larger sample sizes were required to detect a difference.

Holding behaviour and fate

Complimentary analyses focusing on timing-related issues revealed that significant differences in physiology and energetics were associated with different estuarine holding behaviours (S.J. Cooke, unpublished data). We thus grouped fish based on duration of estuarine holding using the 25th and 75th percentiles to yield one group that held for 2 days or less and another group that held for greater than 13 days. Mortality rates clearly differed for these two holding behaviours (Fig. 2). Owing to sample size limitations, we focused additional analyses on the two groups of primary interest that comprised the majority of the fish: the fish that did not hold and died en route and the fish that did hold and successfully reached spawning grounds (i.e., we excluded fish that held and died en route and those that did not hold and reached terminal spawning grounds; Fig. 2). Gross somatic energy had been lower in fish that did not hold and failed to reach spawning grounds, but only significantly for the Adams stock group ($P = 0.035$; Table 3). For females, both 17β-estradiol ($P = 0.019$) and 11-ketotestosterone ($P = 0.038$) hormone titres had been significantly higher in fish that did not hold and died en route compared with fish that held and were successful migrants (Table 3). No other physiological variables were determined to be associated with differences in holding behaviour and subsequent fate. However, statistical power was generally low for most endocrine and stress indicators (i.e., $1 - \beta < 0.70$), as noted for the in-river phase.

Discussion

A segment of late-run Fraser River sockeye salmon populations have altered their migratory behaviour in recent years, initiating their upriver migrations without exhibiting a characteristic marine holding pattern (Cooke et al. 2004*b*; Lapointe et al. 2004). Fish that do not exhibit this holding behaviour experience exceptionally high rates of mortality (Cooke et al. 2004*b*; Lapointe et al. 2004). We found a number of factors that were associated with mortality at different phases of the spawning migration. We discuss these in light

Table 2. Comparison of biological variables between late-run sockeye salmon (*Oncorhynchus nerka*) that entered the river and were detected at Mission, B.C., and either died en route to spawning grounds or arrived at terminal spawning grounds.

Variables	In river en route loss	*N*	Reached natal subwatershed	*N*	Test statistic	*P* value	Observed power	Effect size power
Nose fork length (cm)								
W–H	60.8±0.9	11	61.0±0.5	19	*t*, –0.20	0.846	0.106	0.949
Adams	61.7±0.4	28	61.0±0.3	50	*t*, 1.19	0.238	0.323	1.000
Gross somatic energy (MJ·kg^{-1})								
W–H	7.93±0.29	9	7.91±0.22	17	*t*, 0.06	0.953	0.101	0.291
Adams	8.94±0.17	21	9.23±0.07	40	*t*, –1.79	*0.078*	0.551	0.803
Plasma								
Ions (mmol·L^{-1})								
Na^+	186.4±1.6	24	186.0±1.2	42	*t*, 0.19	0.849	0.106	0.998
K^+	1.54±0.17	24	1.56±0.18	42	*t*, –0.82	0.935	0.101	0.114
Cl^-	148.7±1.2	24	148.5±0.7	39	*t*, 0.19	0.852	0.106	1.000
Osmolality (mosmol·kg^{-1})	346.3±3.4	25	345.8±2.3	42	*t*, 0.13	0.897	0.103	0.997
Cortisol (ng·mL^{-1})	495.7±64.0	25	435.7±40.8	42	*t*, 0.83	0.409	0.212	0.118
Lactate (mmol·L^{-1})	8.89±0.64	25	9.08±0.51	42	*t*, –0.23	0.820	0.109	0.152
Glucose (mmol·L^{-1})	7.01±0.22	25	7.07±0.15	42	*t*, –0.22	0.821	0.109	0.390
Na^+/K^+ ATPase (µmol ADP·mg protein^{-1}·h^{-1})	2.67±0.21	25	2.63±0.14	41	*U*, 0.16	0.878	0.104	0.152
Testosterone (pg·mL^{-1})								
Male	10 113±814	10	10 623±490	16	*t*, –0.57	0.573	0.152	0.157
Female	12 301±1 049	15	11 859±481	26	*t*, 0.44	0.665	0.131	0.161
11-Ketotestosterone (pg·mL^{-1})								
Male	4 998.8±448.6	10	5 412.8±305.9	16	*t*, –0.79	0.437	0.198	0.142
Female	966.5±80.9	15	874.1±37.5	26	*t*, 1.18	0.246	0.315	0.159
17β-Estradiol (pg·mL^{-1})								
Male	415.4±96.7	10	364.1±27.5	16	*t*, 0.62	0.544	0.160	0.109
Female	5 288±607	15	4 313±262	26	*t*, 1.70	*0.097*	0.510	0.129

Note: Fishery losses from the river were excluded from analyses. Multiple analysis of variance revealed that stock differences were only significant for energetics and size variables, so for all other analyses we pooled fish from both the Weaver–Harrison (W–H) and Adams–Thompson–Shuswap (Adams) stock groups. All other analyses represent all late-run sockeye that passed Mission. Reproductive hormones were analyzed by gender. Analyses were conducted using two-sample *t* tests when data were normal and met the homogeneity of variance assumption. Italicized statistical output indicates significant differences at $\alpha = 0.10$. Because we conducted multiple comparisons, Bonferroni corrections were applied and significant values based on this criterion (i.e., $\alpha = 0.008$) would have been bolded. A binomial likelihood test revealed that the number of tests that were significant was fewer than expected by chance ($P = 0.549$). Retrospective power analyses ($1 - \beta$) are reported in two forms. Observed power was calculated using the observed effect size and variance. Effect size power was calculated using a predetermined effect size of 5% and the observed variance.

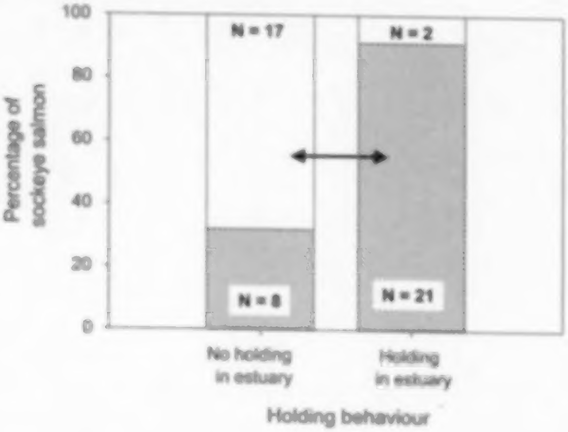
of other information that we have learned about late-run sockeye salmon migration biology obtained from parallel studies.

River entry phase

Approximately 30% of fish tagged failed to reach Mission, B.C., a point 85 km upstream from the river mouth where tidal influence and salt water were no longer present. Based on that finding alone, it is clear that there is significant en route mortality in the coastal environment and the tidally influenced section of the river, not just in the upriver areas. Fish that failed to reach Mission had been more physiologically stressed than fish that did, as revealed by stress indicators (e.g., plasma glucose, lactate, and cortisol). These elevated stress levels are suggestive of elevated energy expenditures (Barton and Schreck 1987) and suppression of reproductive hormones (Kubokawa et al. 2001; Carruth et al. 2002) and hence fitness (Schreck et al. 2001). They also can be responsible for, and immediately precede, mortality (Wood et al. 1983; Farrell et al. 2000).

There is no doubt that capturing fish in a purse seine and holding them on board a research vessel imparted stress. However, it is unlikely that the mortality levels we observed are solely attributable to our interventions (Cooke et al. 2005). For example, when fish were just tagged and not biopsied, there was no difference in either their subsequent mortality rate or their rates of travel from the release site to the river relative to tagged and biopsied individuals (Cooke et al. 2005). Although this is not a direct test of capture-related stress, it does suggest that the stress levels we observed are reflective of a biologically meaningful variation in precapture condition that, as we found, was predictive of en route mortality. In a complimentary study, Cooke et al. (2006) determined that the order of fish sampling–tagging did not influence the fate of summer-run sockeye salmon. Furthermore, we have held ocean-captured sockeye salmon in saltwater laboratory settings to obtain baseline cortisol values (Hinch et al. 2005; A.P. Farrell, unpublished data; e.g., mean ± standard error (SE) plasma cortisol, 354 ± 95 ng·mL^{-1}), and they were comparable with values observed in the current study (e.g., overall mean ± SE plasma cortisol, 435 ± 41 ng·mL^{-1}). Increases in plasma cortisol typically reach peak levels ~1 h after the initial stressor, whereas plasma glucose would be expected to peak about an

Fig. 2. Fate of late-run sockeye salmon (*Oncorhynchus nerka*) in the Fraser River, British Columbia, relative to holding behaviour. Data include late-run fish that entered the Fraser River (excluding fishery removals) with either less than 2 days of holding (no hold) or more than 13 days of holding (hold). Hatched areas indicate successful migrants, whereas open areas represent failed migrants. Numbers indicate the number of fish in each category. The arrow denotes the two primary outcomes for fish (i.e., do not hold in Strait of Georgia and die en route to spawning grounds or hold in Strait of Georgia and successfully reach spawning grounds).



hour after that (Milligan 1996; Mommsen et al. 1999; Barton 2002). Fish captured in the seine net were immediately transferred to an onboard tank (as described in Materials and methods) for temporary holding and sampled within 30 min of capture, so it is unlikely that the cortisol or glucose values obtained reflect differential handling or holding periods. Nonetheless, individuals varied widely in their cortisol levels, suggesting that either fish were experiencing a background level of chronic stress prior to being captured or that the elevation of plasma cortisol during spawning migration of Pacific salmonids is normal (Carruth et al. 2000, 2002). Premature elevation of cortisol could lead to senescence and eventual mortality of salmonids and typically does not occur until after fish have initiated upriver migrations (Carruth et al. 2002).

In addition to the stress indicators discussed above, the plasma Na^+ concentrations were lower in fish that failed to reach the river, whereas plasma osmolality was higher in failed migrants. Hinch et al. (2005) report resting plasma Na^+ (mean ± SE, 185 ± 3 $mmol \cdot L^{-1}$) and osmolality (mean ± SE, 334 ± 17 $mosmol \cdot kg^{-1}$) values for ocean-caught sockeye salmon held in saltwater. The resting plasma Na^+ value from Hinch et al. (2005) is comparable with the value for fish that successfully reached the river (mean ± SE, 186.6 ± 0.9 $mmol \cdot L^{-1}$) and higher than those that died prior to river entry (mean ± SE, 182.5 ± 1.2 $mmol \cdot L^{-1}$). In contrast, the resting plasma osmolality value from Hinch et al. (2005) was lower than both successful (mean ± SE, 345.8 ± 1.8 $mosmol \cdot kg^{-1}$) and especially failed (mean ± SE, 354.9 ± 2.3 $mosmol \cdot kg^{-1}$) river entrants. Generally, when fish experience stress in the marine environment, both plasma Na^+ concentrations and plasma osmolality tend to increase by ~10 units (i.e., either $mmol \cdot L^{-1}$ or $mosmol \cdot kg^{-1}$; Barton et al. 2002). Thus the lower Na^+ and higher osmolality values for failed migrants are biologically relevant but in contradiction, suggesting that the osmoregulatory apparatus and therefore hydromineral balance of failed migrants may be compromised, potentially affecting the salt-to-freshwater transition (Clarke and Hirano 1995). We have documented that variable levels of gill Na^+/K^+ ATPase are characteristic of early entry fish (S.J. Cooke, unpublished data), lending support to the idea that the level of osmoregulatory preparedness for fresh water may influence early entry and subsequent mortality. In brown trout (*Salmo trutta*), osmoregulatory status has been correlated with the initiation of migration behaviour (Aarestrup et al. 2000; Nielsen et al. 2004). An alternative explanation to the contradiction observed between Na^+ and osmolality is that other solutes have affected osmotic pressure, but were not measured in our study (e.g., proteins, sugars, and other ions).

In-river phase

Overall en route (fishery-independent) mortality rates for late-run sockeye between Mission and the terminal spawning grounds were approximately 36% for telemetered fish. When mortality rates for these telemetered salmon were abundance-weighted to account for differences in total late-run river abundance at time of tagging and river entry, en route mortality was 42% (English et al. 2004). However, late-run mortality estimates generated from hydroacoustic counts (Hedgepeth et al. 2000) at Mission (M. Lapointe, Pacific Salmon Commission, Suite 600, 1155 Robson Street, Vancouver, BC V6E 1B5, unpublished data) and arrivals at terminal spawning grounds (minus fishery removals) were much higher in 2003 overall (i.e., ~65%), but this may reflect the fact that we did not telemeter fish in the first 32% of the late-run migration, which were expected to have had even higher mortality. These data provide additional support that our tagging and biopsy technique did not contribute to abnormally high mortality and was reflective of the condition of the fish during the later periods (i.e., after initial 32% of run) of the migration.

The physiological and energetic condition of sockeye salmon intercepted in Johnstone Strait provided limited insight into in-river mortality. Adams late-run sockeye that reached their spawning grounds tended to have a higher somatic energy at time of sampling compared with those that died en route. However, the same trend was not apparent for the W–H fish. Furthermore, the *P* value was 0.078 and thus exceeds the Bonferroni-corrected *P* value of 0.008. Somatic energy reserves are crucial for powering upriver swimming activity (Brett 1995; Rand and Hinch 1998), for egg production (Kinnison et al. 2001, 2003; Patterson et al. 2004), for secondary sexual character development (Hendry and Berg 1999), and for reproductive behaviours (Healey et al. 2003), and low somatic energy can lead to premature energy depletion, en route mortality (Rand and Hinch 1998), and reduced reproductive investment (Hendry and Berg 1999; Kinnison et al. 2001, 2003). Crossin et al. (2004) reported substantial stock-specific differences in somatic energy between fish from the W–H and those from Adams, with the former having lower energy densities than the latter. The fact that we only noted differences in somatic energy among survivors

Table 3. Planned contrast of biological variables for late-run sockeye salmon (*Oncorhynchus nerka*) that entered the river and were detected at Mission, B.C., and either died en route to spawning grounds after not holding in the Strait of Georgia or arrived at terminal spawning grounds after holding in the Strait of Georgia.

Variables	En route loss of no-hold fish	*N*	Fish that reached natal subwatersheds after holding	*N*	Test statistic	*P* value	Observed power	Effect size power
Nose fork length (cm)								
W–H	61.6±0.8	5	61.0±1.5	4	*t*, 0.38	0.717	0.119	0.928
Adams	61.4±0.8	12	60.7±0.6	17	*t*, 0.65	0.524	0.166	0.999
Gross somatic energy (MJ·kg^{-1})								
W–H	7.73±0.37	5	8.55±0.34	3	*t*, –1.49	0.188	0.376	0.260
Adams	8.78±0.22	10	9.33±0.14	14	*t*, –2.25	*0.035*	0.705	0.782
Plasma								
Ions (mmol·L^{-1})								
Na^+	186.6±2.3	11	189.9±2.4	15	*t*, –0.96	0.348	0.242	0.996
K^+	1.43±0.26	11	1.58±0.27	15	*t*, –0.39	0.701	0.124	0.114
Cl^-	146.8±1.8	11	149.5±1.4	13	*t*, –1.18	0.249	0.312	0.999
Osmolality (mosmol·kg^{-1})	346.7±4.7	11	345.8±4.1	15	*t*, 0.14	0.889	0.103	0.998
Cortisol (ng·mL^{-1})	591.7±118.6	11	428.6±50.6	15	*t*, 1.39	0.176	0.387	0.117
Lactate (mmol·L^{-1})	8.90±1.19	11	8.70±1.08	15	*t*, 0.13	0.897	0.103	0.144
Glucose (mmol·L^{-1})	6.69±0.38	11	7.39±0.24	15	*t*, –1.50	0.147	0.425	0.343
Na^+/K^+ ATPase (μmol ADP·mg protein^{-1}·h^{-1})	2.32±0.31	11	2.65±0.17	14	*U*, –0.97	0.344	0.245	0.142
Testosterone (pg·mL^{-1})								
Male	11 567±1 211	5	10 229±1 308	4	*t*, 0.747	0.480	0.176	0.151
Female	13 566±2 066	6	10 935±472	11	*t*, 1.63	0.125	0.464	0.148
11-Ketotestosterone (pg·mL^{-1})								
Male	5 658.5±786.9	5	4 785.5±562.6	4	*t*, 0.86	0.420	0.200	0.147
Female	1 016.1±154.3	6	750.7±26.1	11	*t*, 2.28	*0.038*	0.702	0.145
17β-Estradiol (pg·mL^{-1})								
Male	517.9±169.8	5	395.1±41.3	4	*t*, 0.63	0.551	0.154	1.000
Female	6 029±1 083	6	3 868±659	11	*t*, 2.62	*0.019*	0.804	0.123

Note: Fishery losses from the river were excluded from analyses. Multiple analysis of variance revealed that stock differences were only significant for energetics and size variables, so for all other analyses we pooled fish from both the Weaver–Harrison (W–H) and Adams–Thompson–Shuswap (Adams) stock groups. All other analyses represent all late-run sockeye that passed Mission. Reproductive hormones were analyzed by gender. Analyses were conducted using two-sample *t* tests when data were normal and met the homogeneity of variance assumption. Italicized statistical output indicates significant differences at $\alpha = 0.10$. Because we conducted multiple comparisons, Bonferroni corrections were applied and significant values based on this criterion (*i.e.*, $\alpha = 0.008$) would have been bolded. A binomial likelihood test revealed that the number of tests that were significant was fewer than expected by chance ($P = 0.266$). Retrospective power analyses ($1 - \beta$) are reported in two forms. Observed power was calculated using the observed effect size and variance. Effect size power was calculated using a predetermined effect size of 5% and the observed variance.

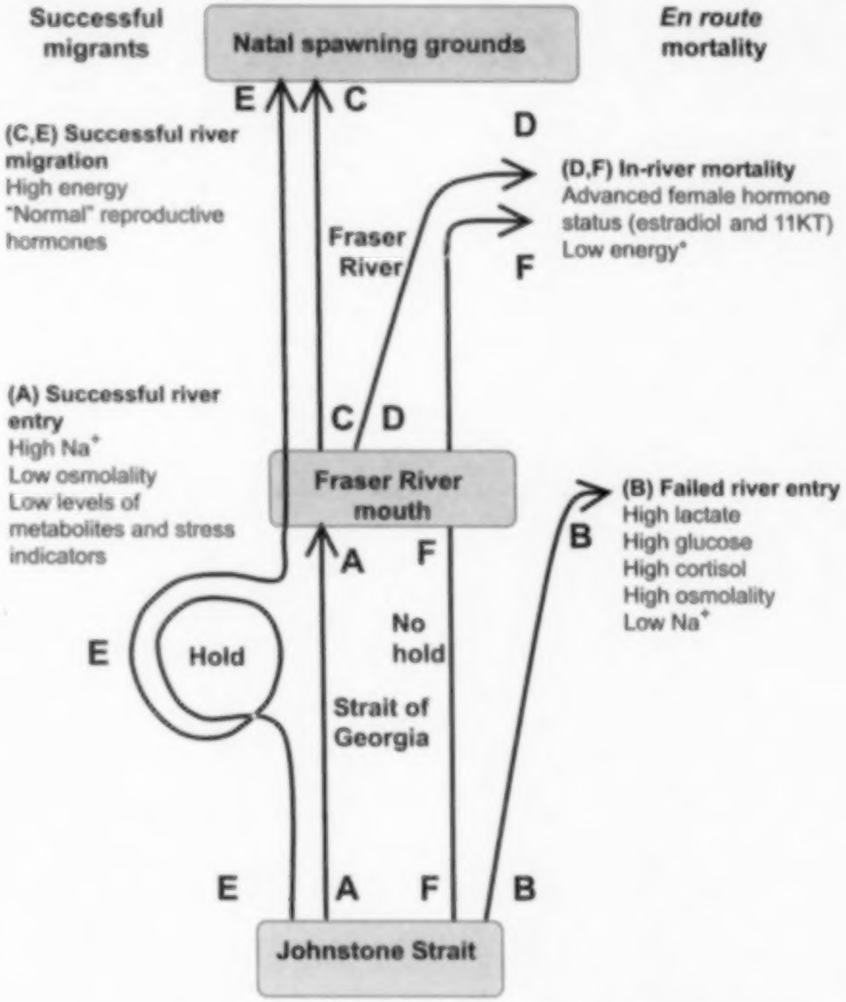
and failed migrants for the Adams group may reflect the fact that W–H fish are under weaker energetic selection because of a less arduous migration (W–H fish make a 161 km river migration and gain ~10 m in vertical elevation; Adams fish make a 485 km river migration and gain ~ 366 m vertical elevation; Crossin et al. 2004).

In this study, females that died en route also tended to have elevated levels of plasma estradiol (marginally significant at $P < 0.10$; i.e., $P = 0.097$), and although none of the other hormone titres in females (i.e., 11-ketotestosterone and testosterone) were significantly different between failed and successful migrants, all three hormone titres were elevated in unsuccessful males. Since these hormones normally increase progressively as salmon mature reproductively (Truscott et al. 1986; Leonard et al. 2002), we interpret these data as indicating that unsuccessful migrants may have been in an advanced state of reproductive development (Robertson 1961; Robertson et al. 1961). Furthermore, given that reproductive development in salmon is associated with a loss in body mass and energy stores (Crossin et al. 2004), the elevated reproductive hormone titres and lower energy reserves of failed migrants may themselves be related and potentially indicate early senescence.

Holding behaviour and fate

Alterations in late-run sockeye salmon behaviour have been correlated with high levels of en route mortality (Cooke et al. 2004*b*; English et al. 2004). Many of our late-run sockeye spent less than 2 days holding in the Strait of Georgia, whereas others held for 2–3 weeks. We therefore pooled these fish accordingly into groups that essentially had no marine holding and those that had at least 2 weeks of marine holding. It turned out that the majority (79%) of our fish fell into one of two groupings: those that did not hold and died en route and those that held and successfully reached spawning grounds. Interestingly, when these two subgroups were contrasted, many of the same physiological differences emerged as we found for the in-river analysis, unlike work on summer-run sockeye (Cooke et al. 2006). Specifically, somatic energy levels tended to be higher in Adams sockeye

Fig. 3. Schematic representation of the behaviour and fate of late-run Fraser River sockeye salmon (*Oncorhynchus nerka*) with associated physiological and energetic profiles. The schematic is ordered from bottom to top reflecting the upstream progression of fish towards terminal spawning grounds. Detailed map of locations can be found in Fig. 1. Also, the physiological and energetic characteristics of fish in each category are provided to the left for successful migrants and to the right for en route mortalities. (A) Fish tagged in Johnstone Strait that achieve successful river entry. (B) Fish tagged in Johnstone Strait that fail to enter the river. Of the fish in A, some of those fish continue onwards and successfully reach spawning grounds (C) or die en route (D). The two primary outcomes for late-run sockeye (i.e., F, do not hold in Strait of Georgia and die en route to spawning grounds; or E, hold in Strait of Georgia and successfully reach spawning grounds) correspond to Fig. 2 and Table 3. The asterisk indicates that gross somatic energy is only significant ($\alpha = 0.10$) for fish from the Adams–Thompson–Shuswap (Adams) group.


Successful migrants
Natal spawning grounds
En route mortality
E
C
D
(C,E) Successful river migration
High energy
"Normal" reproductive hormones
(D,F) In-river mortality
Advanced female hormone status (estradiol and 11KT)
Low energy*
Fraser River
F
(A) Successful river entry
High Na⁺
Low osmolality
Low levels of metabolites and stress indicators
C
D
Fraser River mouth
(B) Failed river entry
High lactate
High glucose
High cortisol
High osmolality
Low Na⁺
A
F
B
No hold
E
Hold
Strait of Georgia
E
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F
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Johnstone Strait

that held prior to migrating and were successful migrants compared with those that did not hold and died en route. Also, females that did not hold and died en route tended to have elevated levels of reproductive hormone titres (both 17β-estradiol and 11-ketotestosterone) relative to fish that had held in the Strait of Georgia and which successfully reached the spawning grounds. Perhaps if we had sampled the leading edge of the late-run migration (i.e., the first 32% of fish), where mortality rates were presumed to be even higher (e.g., Cooke et al. 2004*b*) and the contrast between the length of the holding period was even more extreme, these and other physiological and energetics variables may have exhibited more sharply defined differences.

Conceptual model for early migration – high mortality

The work presented here is not the only attempt to evaluate the physiological and energetic correlates of migration success for sockeye salmon in the Fraser River (e.g., Cooke et al. 2006), but it is the first to focus on the late-run sockeye salmon in an attempt to develop an integrated physiological and energetic understanding, in a migratory stage-specific manner, of the early migration – high mortality phenomenon. During the river entry phase, physiological stress (as measured by cortisol and anaerobic metabolites) affects migration success in late-run and summer-run (Cooke et al. 2006) sockeye. Gross somatic energy was relatively high in summer- and late-run salmon that failed to enter fresh water. During the river migration phase, both summer- and late-run fish that failed to reach spawning grounds exhibited advanced reproductive development, potentially indicative of early senescence. For the river migration phase, failed late-run Adams migrants had lower gross somatic energy, but the same pattern was not observed for the W–H migrants. Collectively, these results suggest that in a given year, the physiological and energetic characteristics of sockeye salmon migrating through Johnstone Strait may be predictive of their fate, irrespective of run-timing group. Cooke et al. (2006) did note higher interstock variation in summer-run fish than we did for late-run fish, suggesting that fish exhibit physiological and energetic diversity at both the individual and the stock level, but that variation is not consistent among run-timing groups or stocks.

Our conceptual model is illustrated in a schematic diagram (Fig. 3) to summarize and illustrate the physiological and energetic characteristics associated with behaviour and fate of late-run sockeye migrants. The factors that contribute to mortality appear to vary with different migratory phases for late-run sockeye salmon. Of particular interest is the contrast between fish that held and survived and those that did not hold and died. As fisheries managers seek predictive tools to determine if and when sockeye will enter early and die en route, physiological tools may be able to provide some insight. If physiological assays could be conducted in near-real time, the predictive value of these tools would be increased. Future studies of this nature should attempt to increase sample size in an effort to increase statistical power (i.e., reduce potential for making a type II error), since we documented substantial interindividual variation (Peterman 1990). Furthermore, attempts need to be made to conduct the same type of research both further from the coastal environment and in the lower river. Indeed, the best predictor may in fact not be apparent when and where we sampled fish. Some variables may have greater predictive power either earlier or later in the migration. Indeed, Hinch et al. (2005) and Shrimpton et al. (2005) report that some physiological variables (e.g., gill Na^+/K^+ ATPase) have already changed in the ocean, in preparation for spawning, at least 500 km from the river mouth. Even though attempts to use physiological data for predictive fisheries management is still some way off, there are already examples of where this is being tested for other species and having reasonable success (e.g., Aarestrup et al. 2000; Nielsen et al. 2004). The current study has revealed physiological differences contributing to the en route mortality of late-run sockeye salmon, providing fisheries managers with some insight into possible mechanisms. However, the ultimate causal factor for mortality may be more related to the reason why some fish are no longer holding (Cooke et al. 2004*b*) and why fish are in different physiological and energetic states. For now, the answers to those difficult questions continue to elude researchers and continue to place these valuable fisheries resources at risk. To address those questions may require focusing efforts on sockeye salmon earlier in their migration when they are still in the high seas environment and later in their migration when they have entered fresh water (e.g., Young et al. 2006). Technological innovations in biotelemetry (Cooke et al. 2004*a*) and the greater coupling of behaviour and physiology should yield additional tools for assessing the migration biology of free-swimming fish and for understanding this fisheries and conservation crisis.

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Protecting marine biodiversity: a comparison of individual habitat quotas and marine protected areas

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Abstract: Fisheries managers in the United States are required to identify and mitigate the adverse impacts of fishing activity on essential fish habitat (EFH). There are additional concerns that the viability of sessile noncommercial species, animals that are habitat dependent and (or) are themselves constituents of fishery habitat, may be threatened by fishing activities. We propose a system of individual habitat quotas (IHQ) to achieve habitat conservation and species protection cost effectively. Individual quotas of habitat impact units would be distributed to fishers with an aggregate quota set to maintain a target habitat "stock". Using a dynamic, spatially explicit fishery simulation model, we explore the efficiency and effectiveness of an IHQ policy versus marine protected areas (MPAs) for conserving habitat-dependent, sessile species of unknown spatial distributions. Our findings indicate that an IHQ policy with a conservatively established habitat target is better suited to the protection of sessile nontarget species than a rotating or fixed MPA policy.

Résumé : Les gestionnaires de la pêche aux États-Unis doivent identifier et mitiger les impacts négatifs des activités de pêche sur l'habitat essentiel des poissons (« EFH »). On se préoccupe aussi de savoir si la viabilité des espèces sessiles non commerciales, qui sont des animaux liés à l'habitat et (ou) eux-mêmes des éléments constitutifs de l'habitat de pêche, puisse être menacée par les activités de pêche. Nous proposons l'établissement d'un système de quotas individuels d'habitats (« IHQ ») afin de réussir à conserver les habitats et à protéger les espèces de façon efficace à un meilleur coût. Des unités de quotas individuels d'impacts sur l'habitat seraient distribuées aux pêcheurs et un quota global fixé de façon à maintenir un « stock » prédéterminé d'habitats. Nous explorons, à l'aide d'un modèle de simulation de la pêche qui est dynamique et explicite en fonction de l'espace, l'efficacité d'une politique d'IHQ par comparaison à l'établissement de réserves marines (« MPA ») pour la conservation des espèces sessiles dépendantes de l'habitat, mais à répartition spatiale inconnue. Nos résultats indiquent qu'une politique d'IHQ avec un objectif conservateur de maintien des habitats est mieux adaptée à la protection des espèces sessiles non ciblées par la pêche qu'une politique de MPA fixe ou en rotation.

[Traduit par la Rédaction]

Introduction

The provisions added to the Magnuson–Stevens Fisheries Conservation and Management Act (MSFCMA) in 1996 require the eight regional fishery management councils to identify and describe essential fish habitat (EFH) in each fishery management plan (FMP), minimize to the extent practical the adverse effects of fishing on EFH, and identify actions to encourage the conservation and enhancement of EFH. In offshore areas, a primary source of habitat damage is commercial fishing, which can reduce the complexity of the benthic structure (Kaiser and de Groot 2000; McConnaughey et al. 2000), increase the resuspension of benthic sediments (Pilskaln et al. 1998), and alter the community and trophic structure within an ecosystem (e.g., Greenstreet et al. 1999; Rice 2000; Schratzberger et al. 2002). These impacts may vary with the type of gear utilized, as well as with the benthic structure (Collie et al. 2000; Johnson 2002; Kaiser et al. 2002).

Although EFH may be characterized in general terms by the type of substrate or depth, in many cases the utility of these habitats for supporting fish populations, and hence the motivation for habitat protection, relates to the presence of various sessile organisms such as corals, sponges, kelp, rockweed, mussels, marine worms, etc. These organisms may have low rates of reproduction and be highly susceptible to habitat damage (North Pacific Fisheries Management Council 2004). In addition, these species may be important to the

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overall integrity of the ecosystem and may have unknown future economic value. Exploring methods of protecting these species is the primary focus of this paper.

Proposed actions to mitigate the impacts of commercial fishing consist mainly of gear restrictions and temporary or permanent area closures (i.e., marine reserves and marine protected areas, MPAs) (Gell and Roberts 2003; Kaiser 2005; Sale et al. 2005). However, there are concerns that EFH protection based on area closures could shift and intensify efforts in other areas threatening species that exist primarily, or solely, in those regions (Kaiser 2005). This may have an adverse impact on nontarget species that are part of or dependent on habitat and on general marine biodiversity in benthic habitats (Pope et al. 2000; Powles et al. 2000; Thrush et al. 2001). In addition, a general lack of knowledge regarding the range of marine species in existence and their distributions makes it difficult to provide adequate protection (Kenchington 2003).

As an alternative approach, we propose an individual habitat quota (IHQ) system to provide habitat protection and to protect sessile nontarget species that are habitat dependent. Whereas individual transferable quotas (ITQs) provide a property right for the stock of a harvestable resource, an IHQ program would be based on the degree of habitat impacts, denoted habitat impact units (HIUs), allowed in a given fishery. Individual quotas of HIUs, based on a proxy for marginal habitat damage resulting from a given fishing activity, would be distributed to fishers with an aggregate quota set to maintain a target habitat "stock" within the fishery. The system is designed to achieve a given average level of habitat quality without dictating the spatial distribution of fishing effort or habitat quality.

To investigate how the IHQ system might perform, we develop a dynamic spatially explicit fishery and habitat simulation model consisting of three primary components: a target species, a habitat stock, and a number of habitat-dependent, sessile, nontarget species. The survival rate of the habitat-dependent species is assumed to depend on whether the habitat quality where they are located is maintained above a specified minimum habitat-quality threshold. Acknowledging the general lack of accurate information regarding the biological characteristics and distributions of sessile organisms in most marine environments, we model a number of stylized sessile organisms with random spatial distributions and varying degrees of global versus local recruitment.

The performance of the IHQ system with different average habitat targets (30% and 50%) is compared with two alternative management regimes, fixed and rotating MPA policies. This extends analysis by Holland and Schnier (2006), which focused simply on the cost effectiveness of achieving a given average level of habitat quality but did not consider the impacts on habitat-dependent species. Our inclusion of habitat-dependent species allows us to explore the relative effectiveness of IHQ and MPAs at conserving a diverse community of habitat-dependent species of unknown spatial distribution.

Materials and methods

An IHQ management system requires the definition and monitoring of habitat impacts that will be allocated and traded. Because it is unlikely to be feasible or cost effective to directly monitor habitat impacts, we propose that a proxy for habitat impacts, denominated in habitat impact units (HIU), be utilized. HIU would represent the marginal damage that the habitat incurs from a single fishing event and would vary depending on the ecological characteristics of the region fished, as well as the amount of fishing that has recently occurred within the region. The habitat impact units used by a vessel might differ with the type of gear utilized and would be based on empirical studies of the marginal physical damage associated with fishing particular gears in particular types of habitat. Suppose, for example, that empirical research showed that a heavily fished area takes 10 years to regenerate to a "pristine" state and that each pass of a bottom trawl over an area removes 80% of the remaining habitat structure. If HIU are denominated in square metres of bottom contacted, a vessel towing a bottom trawl over 10 000 m^2 of "pristine" habitat would use 8000 HIU leaving the proxy for the habitat "stock" in that area at 2000 HIU. If the vessel made a second pass over the same area they would use only 1600 units leaving a stock of 400 HIU. After 1 year, if left unfished, the habitat stock in the 10 000 m^2 area would have increased by 10% of the pristine level of habitat (1000 HIU) leaving a habitat stock of 1400 HIU.

The rate of habitat recovery and damage resulting from fishing activity will invariably be linked to the type of benthic habitat present and the gear utilized (Collie et al. 2000; Hiddink et al. 2006; Kaiser et al. 2006). The use of an 80% habitat reduction, although not identical to recent empirical research, is consistent with recent findings in the literature (Collie et al. 2000; Hiddink et al. 2006). In addition, the 10% recovery rate is similar to the recovery rates of slow-growing biota; however, sandy sediments do recovery much faster (Collie et al. 2000; Kaiser et al. 2006). Given these habitat dynamics and the habitat quota system, it is evident that it is economically cost effective to continually fish in a location previously fished by others because the HIU costs incurred will be lower. In addition, this behavior will generate proportionally less damage then the previous fishing event, which is consistent with the general findings in the literature (Kaiser 2005). However, this will only be rationale provided that the marginal gains from fishing in a region with higher habitat levels are lower than in previously fished locations.

Each year a total quota of habitat units would be set and distributed. Individuals might have an ongoing right to a proportional share of that total quantity or might purchase or be allocated shares of the total quota annually to complement their fishing rights. The total quantity of HIU distributed each year would be set to maintain a given level of habitat protection as measured by the total remaining "stock" of HIU. The total stock of HIU would be made up of a combination of totally and partially regenerated areas. The quantity of HIU allocated each year would depend on the regeneration rate of habitat, the standing stock of habitat, and the target level of the habitat stock. However, the definition of HIU, setting the target stock, and determining the total HIU quota would not require regulators to determine either the total or the marginal value of habitat protection.

HIU use could be monitored remotely using a vessel monitoring system (VMS). For example, trawlers might be charged

HIU any time they are in fishable areas moving within a range of speeds feasible for fishing. More sophisticated systems could be developed using sensors on gear. To be effectively used by fishers, this system would require real-time updating of the state of the habitat. This would not be the true physical state of the habitat but a proxy based on the regeneration rate and when and how much each location had been fished. This information would have to be available to fishers in real time so that they could decide whether fishing in a particular location was worth the HIU they would use to fish there.

Simulation model

To investigate the performance of an IHQ regime, we use a spatially explicit fishery simulation model with a fish stock, habitat stock, fishing effort, and nontarget species stocks modeled on a 25 × 40, two-dimensional grid of 1000 cells. Although a fixed and rotating MPA policy could be simulated using a much coarser spatial resolution (e.g., 3- or 5-patch model), the diffuse and dynamic spatial distribution of habitat protection resulting from IHQs and its implication on cost effectiveness, habitat, and habitat-dependent species would be lost using a coarser spatial resolution.

Following Sanchirico (2004), we use a honeycomb structure to model the physical connectivity of the cells in the grid with diffusion of the target fish stock occurring over the six equal edges of each cell (Fig. 1). Although our model would allow us to explore various forms of spatial heterogeneity in the fishery, we assume homogeneous cost and productivity across all cells to simplify the analysis and avoid compounding effects. To ensure that each cell has the same level of connectivity, we connect the edges of the grid (i.e., target fish can move from the right edge to the left edge and from the top to the bottom and vice versa). This eliminates edge effects associated with the target species aggregating at the edge of the simulation grid and makes the leakage from MPAs independent of their location on the grid. Nontarget species are assumed to be sessile and thus do not move between cells, but both the target species and some of the nontarget species are assumed to exhibit global recruitment spread randomly across the simulation grid.

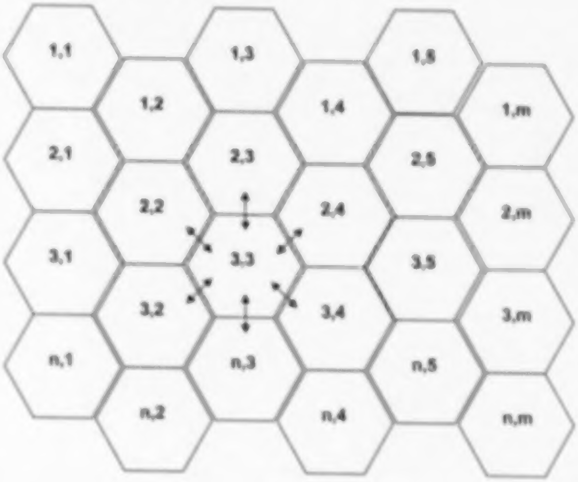
Target and nontarget species dynamics

The populations of the target and nontarget species are similarly modeled as single cohorts, and therefore, we need only track the weight of each species within each cell of the simulation grid. Each year is divided into 50 periods (T = 50). The total catch from cell i in year y and period t is determined by the removals of vessels, v, that choose to fish in location i. The V vessels in the fleet are deployed consecutively within period t, and the population of target and nontarget species is adjusted after each vessel is deployed (Fig. 2). The net change in the target species, x^{Tar}, and nontarget species, x^{Non}, accounts first for the commercial harvest, then growth and recruitment, followed by net population diffusion, and lastly habitat dependence. The capture of the target and nontarget species from each cell i in period t is determined according to

$$x^{M}_{i,y,t,V} = x^{M}_{i,y,t,0} - \sum_{v=1}^{V} q_M e_{i,y,t,v} x^{M}_{i,y,t,v-1} \tag{1}$$

where the weight of fish, x, is indexed by cell i, year y, period t, and vessel deployment v; M indicates target (Tar) or nontarget (Non) species; and $x^{M}_{i,y,t,0}$ represents the respective target and nontarget populations before any fishing takes place. The catchability coefficients for the target and nontarget species, q_{Tar} and q_{Non}, respectively, determine the percentage of the cells population removed by one fishing event and $e_{i,y,t,v}$ takes a value of 1 if vessel v fishes in cell i in year y and period t and a value of 0 otherwise. Note that if one vessel chooses to fish in a given location, the population of the target and nontarget species is reduced before the next vessel is deployed. Therefore, the subsequent capture of both species by a vessel that follows another vessel within the same time period t would be lower than the preceding vessel. A description of how the location choice of each vessel is modeled is discussed in Simulation fleet dynamics.

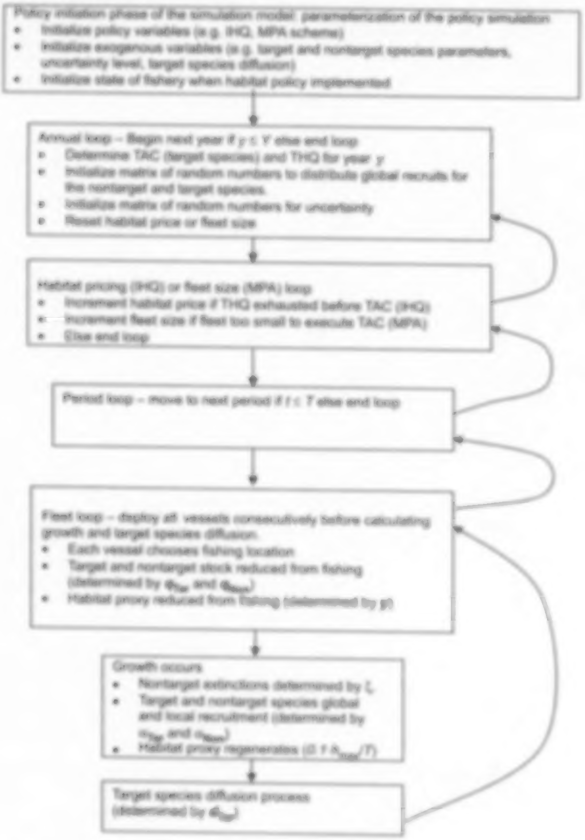
Fig. 1. Spatial structure of simulation model. Fish diffusion takes place across all edges. All cells have the same degree of connectivity since the right and left edges of the grid are connected, as are the top and bottom. For example, in addition to the adjacent cells, cell 2,1 is connected to cells 1,*m* and 2,*m*. Corner cells connect opposite sides and opposite corners. For example, cell 1,1 connects with cells *n*,1, *n*,2, 1,*m*, and *n*,*m*, in addition to the two adjacent cells 2,1 and 1,2.



Total annual growth for the target and nontarget population, G^{Tar} and G^{Non}, respectively, is assumed to follow logistic growth; however, the populations are modeled somewhat differently. The growth of the target species stock is determined by the aggregate population size and carrying capacity, whereas for the sessile nontarget species, growth is dependent on the population in each cell relative to their local carrying capacity. The aggregate annual growth function for the target species at the end of the final time step is

$$G^{\text{Tar}}_{y+1} = \delta_{\text{Tar}} \sum_{i=1}^{N} x^{\text{Tar}}_{i,y,T,V} \left[1 - \frac{\sum_{i=1}^{N} x^{\text{Tar}}_{i,y,T,V}}{K_{\text{Tar}}} \right] \tag{2}$$

Fig. 2. Flowchart of the simulation model. IHQ, individual habitat quota; MPA, marine protected area; TAC, total allowable catch; THQ, total habitat quota.


Policy initiation phase of the simulation model: parameterization of the policy simulation
• Initialize policy variables (e.g. IHQ, MPA scheme)
• Initialize exogenous variables (e.g. target and nontarget species parameters, uncertainty level, target species diffusion)
• Initialize state of fishery when habitat policy implemented
Annual loop – Begin next year if y ≤ Y else end loop
• Determine TAC (target species) and THQ for year y
• Initialize matrix of random numbers to distribute global recruits for the nontarget and target species
• Initialize matrix of random numbers for uncertainty
• Reset habitat price or fleet size
Habitat pricing (IHQ) or fleet size (MPA) loop
• Increment habitat price if THQ exhausted before TAC (IHQ)
• Increment fleet size if fleet too small to execute TAC (MPA)
• Else end loop
Period loop – move to next period if t ≤ T else end loop
Fleet loop – deploy all vessels consecutively before calculating growth and target species diffusion
• Each vessel chooses fishing location
• Target and nontarget stock reduced from fishing (determined by φTar and φNon)
• Habitat proxy reduced from fishing (determined by γ)
Growth occurs
• Nontarget extinctions determined by ζi
• Target and nontarget species global and local recruitment (determined by αTar and αNon)
• Habitat proxy regenerates (0.1 hmax/T)
Target species diffusion process (determined by dTar)

For the sessile nontarget species populations, the annual growth generated by the population in each cell is

$$(3)\qquad G^{\mathrm{Non}}_{i,y+1} = \delta_{\mathrm{Non}}\, x^{\mathrm{Non}}_{i,y,T,V}\left[1 - \frac{x^{\mathrm{Non}}_{i,y,T,V}}{K^{\mathrm{Non}}_i}\right]$$

where $x^M_{i,y,T,V}$ is the biomass of the target or sessile nontarget species in cell i in the final time period T at the end of year y, and δ_M and K^M are their respective intrinsic growth rates and carrying capacities (Table 1). Both the carrying capacity and growth for the sessile nontarget species are indexed by the cell in which the population resides, cell i. For simplification it is assumed that the cell-specific carrying capacity, K^{Non}_i, is constant across all cells.

Growth of the target and nontarget species is modeled differently because of the assumptions that we made regarding each population. The target species is assumed to be mobile and, like most commercial fisheries, is managed with a total allowable catch (TAC) based on the size and surplus production of the aggregate fish stock. Although the spatial distribution of the fish stock might in fact affect growth for many mobile fish stocks, stock assessments rarely account for this and nor do we. We note that this assumption is likely to create some bias in favor of MPAs relative to IHQs, thus providing conservative IHQ results. Modeling the target species growth as a function of density and carrying capacity at the cell level would tend to bias the results against MPAs because total growth would decrease as the population became spatially concentrated in the MPA. In the case of the nontarget species, it makes less sense that growth would be dependent on the entire population relative to a global carrying capacity as we are assuming that these species are sessile and habitat dependent.

Although growth associated with growth of the adult stock is necessarily correlated with the distribution of that stock, growth associated with recruitment need not be. The ratio between the amount of total growth associated with the adult stock and that associated with randomly distributed recruitment is an important characteristic of both target and nontarget species. A locally recruiting species is modeled by maintaining all growth generated by the population in a given cell within that cell. A globally recruiting species is simulated by allowing a share of total growth to be distributed randomly over the entire model grid.

In the simulation model, the division of local versus global recruitment is achieved by dividing total annual growth into two components, growth from recruitment and growth of the existing population. Parameters α_M (M = Tar or Non) determine the share of the total growth for the target and nontarget species, respectively, that occurs through the growth of its constituent population. For the five stylized sessile organism classes, we vary α_M from 1 to 0 using equal spacing over this interval for the five classes (Table 2). For the target species, we assume an equal split between the adult growth and recruitment, $\alpha_{\mathrm{Tar}} = 0.5$.

For the target species, growth of the adult population is distributed evenly throughout the year and among the cells in direct proportion to their share of the overall population. This is represented by the second term in eq. 4. Growth from global recruitment is distributed randomly, both over space and through the year, and is captured by the third term in eq. 4:

$$(4)\qquad x^{\mathrm{Tar}}_{i,y,t+1,0} = x^{\mathrm{Tar}}_{i,y,t,V} + \alpha_{\mathrm{Tar}}\left[\left(\frac{G^{\mathrm{Tar}}_y}{T}\right)\frac{x^{\mathrm{Tar}}_{i,y,t,V}}{\sum_{i=1}^{N} x^{\mathrm{Tar}}_{i,y,t,V}}\right] + (1-\alpha_{\mathrm{Tar}})\frac{G^{\mathrm{Tar}}_y\, z^{\mathrm{Tar}}_{i,y,t}}{\sum_{i=1}^{N}\sum_{t=1}^{T} z^{\mathrm{Tar}}_{i,y,t}}$$

where T is the number of time steps modeled in each year (50), N is the number of locations within the simulation grid (1000), and $z^{\mathrm{Tar}}_{i,y,t}$ is a randomly distributed number between 0 and 1 assigned to each cell, year, and period and captures the random settlement of recruits.

For the sessile nontarget species, the division of growth is similar yet it occurs at the cell level and is determined as follows:

Table 1. Target species parameters.

Parameter	Value
Growth rate (δ_{Tar})	0.40
Carrying capacity (K^{Tar})	2 000 000
Adult growth share of total growth (α_{Tar})	0.50
Fish catchability coefficient (φ_{Tar})	0.40
Habitat catchability coefficient (γ)	0.80
Maximum annual habitat regeneration rate per cell (rT)	$0.1 \cdot h_{max}$
Price of fish (p^f)	1.00
Diffusion rates (d_{Tar})	0.01–0.03
Uncertainty multiplier (σ)	0.0–0.25
Fleet size	10 for IHQ, variable for MPA

Table 2. Sessile nontarget species parameters.

	Sessile class				
Parameters	1	2	3	4	5
Growth rate (δ_{Non})	0.03	0.03	0.03	0.03	0.03
Cell-specific carrying capacity (K_i^{Non})	300	300	300	300	300
Local vs. global recruitment rate (α_{Non})	1	0.75	0.5	0.25	0
Catchability coefficient (φ_{Non})	0.05	0.05	0.05	0.05	0.05
Number of species simulated	20	20	20	20	20

$$(5) \qquad x^{Non}_{i,y,t+1,0} = x^{Non}_{i,y,t,V} + \alpha_{Non}\left[\left(\frac{G^{Non}_{i,y}}{T}\right)\right] + (1-\alpha_{Non})\frac{z^{Non}_{i,y,t}\sum_{i=1}^{N} g^{Non}_{i,y}}{\sum_{i=1}^{N}\sum_{t=1}^{T} z^{Non}_{i,y,t}}$$

where all variables are as defined earlier. Note that the component resulting from adult growth is simply a percentage of the surplus production from the individual cell, whereas recruitment is a randomly determined percentage of aggregate recruitment from the entire multicell population. To ensure that the random distributions of the target and nontarget populations are uncorrelated, separate "seeds" are used for the random number generator.

The nontarget species are assumed to be sessile and therefore do not move between cells, but the target stock is assumed to move among the cells according to a diffusion process. Net diffusion is modeled as

$$(6) \qquad x^{Tar}_{i,y,t+1,0} = x^{Tar}_{i,y,t,V} + d_{Tar}\left(\sum_{k=1}^{6} x^{Tar}_{k,y,t,V} - 6x^{Tar}_{i,y,t,V}\right)$$

where d_{Tar} represents the diffusion rates for the target species and $x^{Tar}_{k,y,t,V}$ is the target population level in the six surrounding cells.

The spatial dynamics of the nontarget species includes one additional complexity, the degree of habitat dependence possessed by the species. Utilizing a habitat threshold variable, ξ, the survival of the population of the nontarget species in each cell is determined by

$$(7) \qquad x^{Non}_{i,y,T,V} = \begin{Bmatrix} x^{Non}_{i,y,T,V} & \text{if} & h_{i,y,T,V} \geq \xi \\ 0 & \text{if} & h_{i,y,T,V} < \xi \end{Bmatrix}$$

where $h_{i,y,T,V}$ represents the habitat level in location i in time period T and year y following vessel deployment V. Within the simulations, ξ is varied between 0% and 10% of the "pristine" habitat level.

The spatial distributions of the target and nontarget species were initialized differently. The target species was randomly distributed throughout the 1000 grid cells within the simulation model and then "smoothed" by repeating the diffusion process expressed in eq. 6 until the spatial distribution possessed only a small degree of variability. For each sessile nontarget species (20 in each class), its spatial distribution was created by randomly assigning the entire population (totaling 33.33% of the global carrying capacity) to 25 cells and then repeating the same "smoothing" process but curtailing it to allow distinct peaks in the spatial distribution to persist. Our rationale for distributing the nontarget species in this manner was to create a spatial distribution that was random but patchy. This distribution would presumably correspond with an ecologically sensitive nontarget species with a limited and spatially defined niche in the ecosystem. In addition, each nontarget species was initialized with a separate random distribution.

Simulation habitat dynamics

The habitat stock h in each cell is modeled simply. We assume that each cell has a homogeneous maximum habitat stock level of h_{MAX} and that habitat regenerates at a fixed rate of recovery, r, per a time step, t, which is capped at the maximum habitat stock level. As was the case with the target and nontarget populations, the habitat stock is consecutively depleted by each vessel that chooses to fish within the location:

$$(8)\qquad h_{i,y,t+1,0} = h_{i,y,t,0} - \sum_{v=1}^{V} \gamma e_{i,y,t,v}\, h_{i,y,t,v-1} + \min[(h_{\mathrm{MAX}} - h_{i,y,t,v}), r]$$

where γ is the marginal rate of habitat damage, $h_{i,y,t,0}$ is the habitat quality in cell i in year y in time period t before any fishing activity, whereas $h_{i,y,t,v}$ is the corresponding habitat quality after fishing event v, and $e_{i,y,t,v}$ is a binomial indicating a fishing event occurring as defined earlier. Each year the total quota for habitat is set equal to the projected habitat level at the end of the year in the absence of fishing less the target level for the habitat stock. This maintains the habitat stock at the "target" level, yet allows its spatial distribution to be endogenously determined by the fleet. The total habitat quota (THQ) of HIU, which is distributed evenly among the fleet, is calculated as

$$(9)\qquad \mathrm{THQ}_y = -H^{\mathrm{Tar}} + \sum_{i=1}^{N} [h_{i,y-1,T,V} + \min[(h_{\mathrm{MAX}} - h_{i,y-1,T,V}), rT]]$$

Simulation fleet dynamics

Vessels are assumed to be motivated solely by profit. Their location choice decisions do not depend directly on the effect they have on the nontarget species but they do depend on charges for habitat impacts. Each year the TAC for the target species is set equal to the growth of the target population, G^{Tar}, plus any residual unfished quota from the previous year. The model ensures that the fleet captures between 99.5% and 100% of the target species TAC each year, and because growth is deterministic, the TAC is effectively constant. Fish and habitat quota is divided evenly among the fleet. The spatial distribution of effort within the fishery is determined by a looping process. Initially, the price of habitat is set equal to zero and the vessels are consecutively distributed to the areas within the fishery with the highest expected profit, the difference between HIU costs and relative expected revenues rates. The expected profits for each vessel in each area are calculated as

$$(10)\qquad \pi_{i,y,t,v} = p^f q_{\mathrm{Tar}} X^{\mathrm{Tar}}_{i,y,t,v} \exp(\sigma \varepsilon_{i,y,t,v}) - p^h \gamma h_{i,y,t,v}$$

where p^f and p^h are the price of fish and habitat, respectively, σ is an uncertainty multiplier, and $\varepsilon_{i,y,t,v}$ is a normally distributed random number with mean 0 and standard deviation 1. Because vessels fish consecutively and vessels fishing in a given location remove 40% of the fish in that location, it is unlikely that two vessels fish in the same location during the same period. The larger the uncertainty multiplier, the greater is the uncertainty each vessel faces with respect to the expected catch and revenues realized within a given location, thereby increasing the probability that a vessel's spatial choice deviates from the true optimum. However, this multiplier only affects a vessel's expectations; the actual catch realized is deterministic.

If the target TAC is not completely used up because the THQ is exhausted first, then the HIU price is increased and the year is simulated again. This looping process continues until a price for HIU is found that allows the fleet to catch the entire TAC without exhausting the total quota for habitat. Although our primary interest is the impact that the IHQ has on the viability of the nontarget species, it is still integrally important that we determine the optimal HIU price because different prices yield different spatial distributions of effort. Alternative spatial distributions result in different impacts on the habitat and nontarget species than that which corresponds with the optimal HIU value. The MPA simulations allow the fleet size to change so that the fleet size is adequately large, but the minimum size necessary, to take the TAC. The minimum fleet size is determined through a looping process similar to that used to determine the price of HIU for the IHQ policy scenarios.

Simulation policy evaluation

All simulations begin with the same initial distribution and size of the fish population and habitat resulting from running the model for 20 years with a TAC equal to that used for subsequent years, but no habitat regulations. The habitat management policy is then implemented and the simulation continues for an additional 50 years. After year 20, the IHQ model sets the initial target for the total habitat stock equal to the minimum of the habitat target specified by the policy or the current habitat stock plus an increment of 2% of the virgin level. The habitat target is then increased in this way each year until it reaches the final habitat target (either 30% or 50% of the pristine level), where it remains for the rest of the simulation.

For the fixed MPA model, after the 20-year initialization, a vertical, 25 × 8 strip of cells encompassing 20% of the fishery is closed to fishing and remains closed for the duration of the simulation. Given that there are 100 different sessile organisms simulated, each with a spatially distinct distribution, MPA site selection cannot be determined by the one that yields the "best" protection for all the species. Therefore, MPA 3 was arbitrarily selected as the fixed MPA (Fig. 3). The rotating MPA model functions similarly but rotates the closed area every 10 years of the simulation. The rotating closures are ordered such that each new closure is nonadjacent to the last (Fig. 3).

To test the sensitivity of our simulations, we vary three key parameters: the nontarget species habitat threshold ξ, the rate of target species diffusion, and the degree of uncertainty that fishers face regarding the distribution of the target species. Other target species parameters (Table 1) are fixed for all the simulations. For the five subclasses of sessile nontarget species, biological parameters were fixed but the degree of global versus local recruitment differed across the subclasses (Table 2). The parameters were selected not to mimic a specific nontarget species, but to represent a broad class of species characteristics.

Results

The cost effectiveness of the four policies can be evaluated by comparing the catch-per-unit-effort (CPUE) obtained under each of the four policies. Since total catch and its value are constant under all policies and harvest costs are solely a function of nominal effort, a higher CPUE directly

Fig. 3. Diagram of area closures for marine protected areas (MPAs). For fixed MPAs, MPA 3 remains closed for the entire simulation. For rotating MPAs, areas are closed for 10 years and then reopened in numerical order.

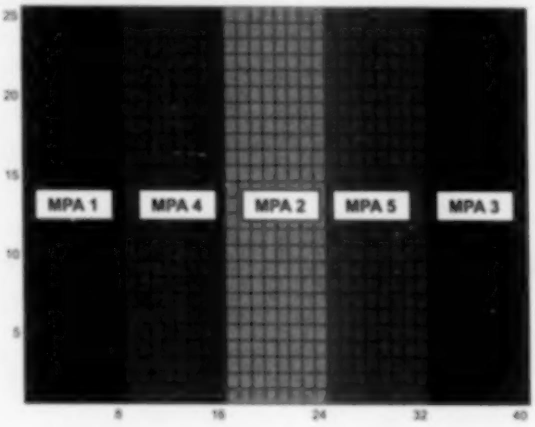


Table 3. Ratio of after-policy catch-per-unit-effort (CPUE) (average over years 21 through 70) to before-policy CPUE (average over years 1 through 20) with varying rates of diffusion and uncertainty.

	Uncertainty		
Target species diffusion	0.00	0.125	0.25
CPUE ratio: fixed MPA			
0.01	0.46	0.46	0.45
0.02	0.83	0.83	0.82
0.03	0.90	0.90	0.89
CPUE ratio: rotating MPA			
0.01	0.96	0.97	0.97
0.02	0.93	0.93	0.94
0.03	0.94	0.94	0.94
CPUE ratio: IHQ_30			
0.01	1.00	1.00	0.99
0.02	1.00	1.00	1.00
0.03	1.00	1.00	1.00
CPUE ratio: IHQ_50			
0.01	0.99	0.90	0.98
0.02	1.00	1.00	0.99
0.03	1.00	1.00	0.99

Note: The first two sections indicate results for the fixed and rotating marine protected areas (MPAs). The final two sections indicate results for the individual habitat quota (IHQ) policy with a 30% (IHQ_30) and 50% (IHQ_50) habitat target.

translates to a proportionally lower harvest cost and higher profitability. Because CPUE varies with the diffusion rate and uncertainty with no habitat protection in place, we present the average CPUE for the four policies simulated (for years 21–70) as a ratio of the average CPUE obtained within the simulation before the implementation of the policy (for years 1–20). CPUE is only marginally reduced by the IHQ regime and this result is robust to both the rates of diffusion and uncertainty (Table 3). In the IHQ model with a 30% habitat target (IHQ_30), CPUE was maintained at more than 99% of the pre-IHQ level regardless of the rate of diffusion or degree of uncertainty. In the IHQ model with a 50% habitat target (IHQ_50), CPUE was maintained at more than 97% of the pre-IHQ level. The greatest relative reductions occur at the highest level of uncertainty.

CPUE results for the MPA regimes are always below those of either IHQ regime, but the rotating MPA policy maintains a higher CPUE than the fixed MPA. With a rotating MPA, CPUE is maintained at 93% to 96% of pre-MPA levels but ranges from 46% to 90% for the fixed MPA. Higher diffusion generates a larger decrease in CPUE for the rotating MPA policy, whereas higher uncertainty has the opposite effect, but neither causes a large difference in CPUE. Diffusion has a greater impact on CPUE within the fixed MPA model. Assuming no uncertainty, CPUE rises from 46% to 90% of pre-MPA levels as the diffusion rate increases from 0.01 to 0.03. When diffusion is 0.01, the fleet size required to capture the TAC doubles within the first 20 years, greatly increasing the total nominal effort. This results because the target species concentrates within the MPA and few individuals spill over into the fishing grounds. For the fixed MPA policy, uncertainty has a relatively small impact on CPUE, causing it to fall from 46% to 45% of the pre-MPA level as the rate of uncertainty increases from 0.0 to 0.25, assuming a diffusion rate of 0.01.

Although the price of HIU may be irrelevant from a public cost–benefit perspective because it represents only a wealth transfer rather than an increase in real cost, it may be of great importance to an individual who has to purchase HIU or has the opportunity to lease or sell their allocation. With no uncertainty, the price of HIU is very low, but it rises steeply with increasing uncertainty resulting in a 19- to 32-fold increase depending on the diffusion rate (Table 4). Diffusion rates also influence the price of HIU, with high diffusion rates causing the price to fall (Table 4). However, uncertainty has the largest impact on the price of HIU. Increasing the habitat target also results in a substantially higher price. Holding the level of target species diffusion at 0.01, the HIU price increases between 200% and 300%, depending on the uncertainty level present, as the habitat target is increased from 30% to 50%.

Our primary focus is on the ability of different habitat protection policies to preserve sessile nontarget populations, and we provide a detailed discussion of those results below. However, it is important to note that the different policies also lead to significantly different levels of average habitat quality. The IHQ regime sets and maintains an average habitat quality but does not dictate the spatial distribution of habitat impacts and quality. In contrast, the average habitat quality of the fixed and rotating MPA regimes varies with the diffusion rate of the target species and uncertainty. Average habitat quality for the fixed MPA varies between 20% and 40% of the maximum depending on the level of diffusion and uncertainty. With the lowest diffusion rate, average habitat quality for the entire grid is maintained at a minimum of 20% by the MPA, but habitat quality outside the MPA approaches zero. This is due to the increased level of effort required to take the TAC when diffusion is low. The rotating MPA results in an average habitat quality ranging from 25% to 33% of the maximum. As with fixed MPAs,

Table 4. Average habitat quota prices (HIUs) for the individual habitat quota IHQ policies with 30% (IHQ_30) and 50% (IHQ_50) habitat targets, assuming various rates of diffusion and uncertainty for the target species.

	Uncertainty		
Target species diffusion	0.00	0.125	0.25
Habitat price : IHQ_30			
0.01	0.006	0.075	0.182
0.02	0.003	0.050	0.123
0.03	0.002	0.040	0.103
Habitat price : IHQ_50			
0.01	0.017	0.154	0.391
0.02	0.005	0.115	0.317
0.03	0.004	0.104	0.284

higher diffusion rates lead to higher average habitat quality. However, average habitat quality fluctuates, falling substantially in the 2–3 years after rotation and then rebuilding until the next rotation.

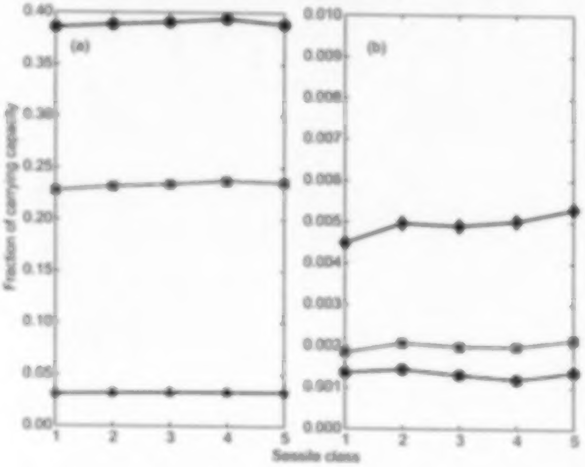
Sessile nontarget species impacts

Although all nontarget species populations are initialized at one-third of their carrying capacity, for habitat thresholds above zero they are already substantially reduced before a habitat protection policy (IHQ or fixed or rotating MPA) is implemented in year 20 (Fig. 4). Because the catchability coefficient for the nontarget species is low, the population reductions are mainly a result of habitat loss rather than bycatch mortality. The higher the habitat threshold, the more the nontarget species populations are reduced, prior to the policies are implemented. The largest absolute reductions in nontarget populations occur when the habitat threshold is increased from 2% to 4%, but the greatest relative reductions occur when the habitat threshold increases from 2% to 4% and from 4% to 6%. The nontarget populations are reduced on average by 86% as the habitat threshold increases from 2% to 4% and a further 85% for an increase from 4% to 6%. Higher habitat thresholds further reduce the nontarget species population, but most of the significant population reductions occur as the threshold is increased from 0% to 6%. This result is linked to the habitat catchability coefficient, which reduces a "pristine" area to a 4% level following two consecutive fishing events in the same location. Given that habitat regenerates between time steps, a slightly higher habitat level may arise if the fishing events do not immediately follow each other. However, if the 6% habitat threshold is in place, these marginal improvements are eliminated.

Population levels before habitat protection are also affected, though less dramatically, by the diffusion rate of the target species and uncertainty in its distribution. In some cases, when the nontarget species has a 10% habitat threshold, it has been pushed to extinction even before the policy is implemented (where we define extinction as a population level that does not exceed 0.1% of the carrying capacity). Most of these extinctions occur at the lowest target species diffusion rate and are marginally mitigated by uncertainty.

Before-policy population levels are relatively similar across the five sessile classes, but the effectiveness of habitat protection measures vary considerably both by the type of protection and across species classes. Assuming a 6% habitat threshold, the rotating MPA and IHQ_30 provide the least protection (Table 5) for nontarget species. Table 5 focuses on the before- and after-policy population levels for a 6% habitat threshold because this is the juncture at which the ratio of the habitat catchability coefficient to the habitat threshold becomes critically binding on the survival of the nontarget species. Results for the rotating MPA are not illustrated in Table 5 because in all cases the after-policy population levels are below the extinction threshold. For the fixed MPA policy, the after-policy population reductions are the greatest for sessile class 5 and least for sessile class 2. The IHQ_50 after-policy population reductions are the greatest for sessile class 1 and least for sessile class 3. In fact, the IHQ_50 policy resulted in an increase in the sessile class 3 population levels. The largest of these increases occurred when the target species diffusion rate was small (0.01) and the degree of uncertainty was high (0.25).

Fig. 4. Before-policy mean sessile class populations in year 20 expressed as a fraction of the global carrying capacity under various habitat threshold assumptions (Hab 0% to Hab 10%). Target species diffusion = 0.02 and uncertainty = 0.125 ((*a*) circles, Hab 0%; squares, Hab. 2%; stars, Hab 4%; (*b*) diamonds, Hab 6%; squares, Hab 8%; circles, Hab 10%).



These results are driven by the degree of global versus local recruitment that characterizes each sessile class. Sessile classes 1 and 2 are predominately local recruiters. This decreases the probability that their recruits will settle in areas with insufficient habitat and favors the use of a fixed MPA because it provides adequate protection for the population and assures that the recruits settle in areas with sufficient habitat. If the species is predominately a global recruiter (sessile classes 4 and 5), the probability of the recruits settling in areas with poor habitat is increased. Thus, the fixed MPA provides a lower level of protection for these species classes.

These characteristics also explain the IHQ_50 policy results. The IHQ_50 policy maintains a higher average habitat quality than any of the other policies, but the spatial distribution of the habitat is not as temporally consistent as the fixed

Table 5. Average ratio of nontarget populations at year 20 relative to the initialized levels assuming a 6% habitat threshold and percentage changes from average population size at year 20 under alternative habitat protection with varying target species diffusion and uncertainty.

		Average % reduction by year 70 from population size at year 20		
Sessile class (diffusion, uncertainty)	Year-20 population	Fixed MPA	IHQ_30	IHQ_50
Sessile class 1				
(0.01, 0)	0.008	Ext	Ext	–38.5
(0.01, 0.25)	0.013	–53.5	Ext	–4.7
(0.03, 0)	0.027	–33.0	Ext	–26.4
(0.03, 0.25)	0.023	–52.6	Ext	–59.0
Sessile class 2				
(0.01, 0)	0.007	Ext	–50.0	0
(0.01, 0.25)	0.014	–33.3	Ext	35.6
(0.3, 0)	0.027	–5.5	Ext	–1.1
(0.3, 0.25)	0.023	–37.2	Ext	–34.6
Sessile class 3				
(0.01, 0)	0.007	Ext	–54.2	4.0
(0.01, 0.25)	0.014	–43.8	Ext	35.4
(0.03, 0)	0.027	–4.4	Ext	9.9
(0.03, 0.25)	0.024	–40.5	Ext	–27.9
Sessile class 4				
(0.01, 0)	0.008	Ext	Ext	–8.0
(0.01, 0.25)	0.014	–52.2	Ext	30.4
(0.03, 0)	0.027	–14.4	Ext	6.7
(0.03, 0.25)	0.023	–46.8	Ext	–28.9
Sessile class 5				
(0.01, 0)	0.007	Ext	Ext	–26.1
(0.01, 0.25)	0.014	–70.8	Ext	6.3
(0.03, 0)	0.027	–30.0	Ext	–11.1
(0.03, 0.25)	0.024	–59.5	Ext	–40.5

Note: Ext indicates that the species went extinct because the population did not exceed 0.001 of the global carrying capacity within the fishery.

MPA. Under the IHQ_50 policy, a specific location may maintain a high habitat level indefinitely. However, a location with high habitat quality may be fished if the opportunity costs of preserving the location become too high. Therefore, a species with a mixture of local and global recruitment is better protected by the IHQ_50 because it concentrates some growth in unfished locations with high habitat quality and is capable of resettling an area after it is fished. Sessile class 3 strikes this balance between a sufficient level of local recruitment to sustain the population in the good habitat regions and its ability to resettle surrounding areas after habitat has regenerated after a fishing event.

Another important concern regarding the protection of sessile nontarget species is the number of extinctions that result under the four policies simulated. Although the extinction threshold we have selected is arbitrary, it does provide a benchmark of comparison across the four policies. The total number of extinctions under each policy is illustrated as the habitat threshold increases from 6% to 10%, with the maximum number of extinctions possible for each class being 20 (Table 6). The two policies that result in the lowest number of extinctions are the fixed MPA and IHQ_50 management regimes. The rotating MPA policy failed to protect any nontarget species from extinction by year 70 for habitat thresholds of 6% or higher. The IHQ_30 policy resulted in the second largest number of extinctions and only provided adequate protection when the habitat threshold was less than 6%.

The fixed MPA and IHQ_50 management regimes provide consistent protection from extinction at the 6% habitat threshold, except at the lowest diffusion rate ($d_{\mathrm{Tar}} = 0.01$) and no uncertainty ($\sigma = 0$) for the fixed MPA, but falter at the higher habitat thresholds. The increase in extinctions is highest with low target species diffusion, which often results in the complete extinction of the sessile class. Sessile classes that were either purely local or global recruiters also yielded the largest number of extinctions, indicating that species at either end of the local versus global recruitment spectrum are difficult to protect regardless of the policy selected.

The relative performance of the different habitat protection measures in terms of average nontarget population levels maintained also vary greatly across policies, species classes, target species diffusion rates, and uncertainty levels. Results for sessile classes 1, 3, and 5 are illustrated as the habitat threshold of the nontarget species increases from 0% to 10% of the pristine habitat level (Figs. 5–7). Results are expressed as a ratio of the mean population level of each policy ($20 < y \leq 70$) to that maintained under the IHQ_50

Table 6. Number of extinctions (population in year 70 < 0.001 of the global carrying capacity) for each sessile organism class under various levels of target species diffusion and uncertainty.

Sessile class (diff., uncert.)	6% Habitat threshold				8% Habitat threshold				10% Habitat threshold			
	Fix.	Rot.	IHQ_30	IHQ_50	Fix.	Rot.	IHQ_30	IHQ_50	Fix.	Rot.	IHQ_30	IHQ_50
Sessile class 1												
(0.01, 0)	20	20	14	0	20	20	20	20	20	20	20	20
(0.01, 0.25)	1	20	20	0	20	20	20	20	20	20	20	20
(0.03, 0)	0	20	20	0	0	20	20	0	20	20	20	20
(0.03, 0.25)	0	20	20	0	1	20	20	20	6	20	20	20
Sessile class 2												
(0.01, 0)	20	20	20	0	20	20	20	20	20	20	20	20
(0.01, 0.25)	0	20	20	0	20	20	20	1	20	20	20	20
(0.03, 0)	0	20	20	0	0	20	20	0	20	20	20	20
(0.03, 0.25)	0	20	20	0	0	20	20	14	1	20	20	20
Sessile class 3												
(0.01, 0)	20	20	6	0	20	20	20	20	20	20	20	20
(0.01, 0.25)	0	20	20	0	20	20	20	4	20	20	20	20
(0.03, 0)	0	20	20	0	0	20	20	0	20	20	20	20
(0.03, 0.25)	0	20	20	0	0	20	20	0	1	20	20	20
Sessile class 4												
(0.01, 0)	20	20	11	0	20	20	20	20	20	20	20	20
(0.01, 0.25)	0	20	20	0	20	20	20	4	20	20	20	20
(0.03, 0)	0	20	20	0	0	20	20	0	20	20	20	20
(0.03, 0.25)	0	20	20	0	0	20	20	2	5	20	20	20
Sessile class 5												
(0.01, 0)	20	20	20	0	20	20	20	20	20	20	20	20
(0.01, 0.25)	0	20	20	0	20	20	20	10	20	20	20	20
(0.03, 0)	0	20	20	0	0	20	20	0	20	20	20	20
(0.03, 0.25)	0	20	20	0	8	20	20	11	18	20	20	20

Note: diff., target species diffusion; uncert., uncertainty; Fix., fixed; Rot., rotating.

policy. Each row in the figures represents a different level of target species diffusion (d_{Tar} = 0.01, 0.02, and 0.03) and each column represents the degree of uncertainty regarding the target species distribution (σ = 0, 0.125, and 0.25). It should be noted that with the higher habitat thresholds, the populations are already near extinction before the policies are implemented. To facilitate the graphical comparison of the policies, when the mean population goes extinct, it is assigned a value equal to the extinction threshold. Therefore, if all the policies result in extinction, they are indistinguishable from each other.

In general, the target species diffusion rate has a negative impact on the population of each sessile class at the lower habitat thresholds ($0 < \xi \le 6$) and a positive effect at the higher habitat thresholds ($\xi > 6$). For instance, under the IHQ_50 policy, increasing the target species diffusion rate from 0.01 to 0.03 decreases the sessile class 1 population by 62.86%, assuming a habitat threshold of 2% and uncertainty of 0.125. For sessile classes 3 and 5, the corresponding decreases are 57.93% and 56.78%, respectively, indicating that higher degrees of global recruitment mitigate the effect of target species diffusion. When the habitat threshold is 8%, these results are reversed as they rebound from extinction levels when diffusion is equal to 0.01 to a population level over twice the extinction level when diffusion equals 0.03.

Higher rates of diffusion cause effort to be more evenly spread out, which increases the probability that a site will be fished at least once within a given year. However, because effort is more evenly spread out, the probability that a site is fished repeatedly within a season is lower than if the target species was more concentrated. When the habitat threshold increases above the 6% level, the sessile population levels begin to increase again as the risk of a site being fished twice consecutively is reduced. An exception to this occurs with the fixed MPA if the habitat threshold is zero, where a higher rate of diffusion increases all the sessile class populations. For sessile classes 1, 3, and 5, increasing diffusion from 0.01 to 0.03 and holding uncertainty at 0.125 increases the population level by 18.47%, 18.99%, and 18.94%, respectively. This result is driven by the fact that the fleet size required to catch the target species TAC at the lowest rate of target species diffusion is nearly five times that required to catch the TAC at the higher rates of diffusion. This lowers the number of fishing events and therefore the amount of nontarget species captured as bycatch.

Comparing the four policy regimes, increasing the target species diffusion rate increases the performance of the fixed MPA relative to the IHQ_50 model. These differences are most pronounced for sessile class 1 in which the fixed MPA yields a mean population greater than the IHQ_50 regime in a number of cases (Fig. 5), but differences are dampened as the degree of global recruitment increases (Figs. 6 and 7). The target species diffusion rate has no consistent impact on performance of the IHQ_30 and rotating MPA relative to the

Fig. 5. Mean sessile class 1 population as a ratio of IHQ_50 population. Lines with circles represent the fixed marine protected area (MPA) policy, lines with squares represent the rotating MPA policy, lines with diamonds represent the IHQ_30 policy, and the solid line represents the IHQ_50 policy (Dif., target species diffusion; Unc., uncertainty).

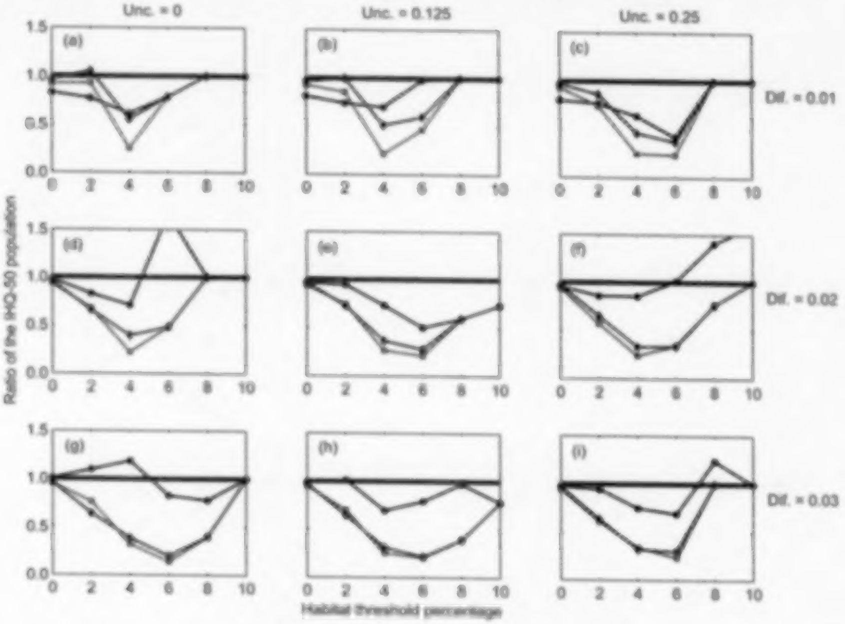
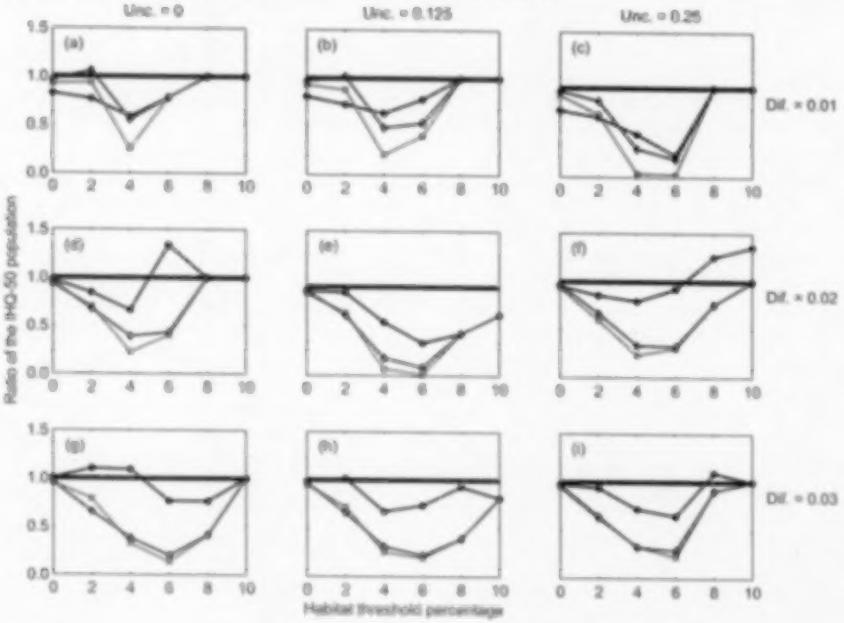


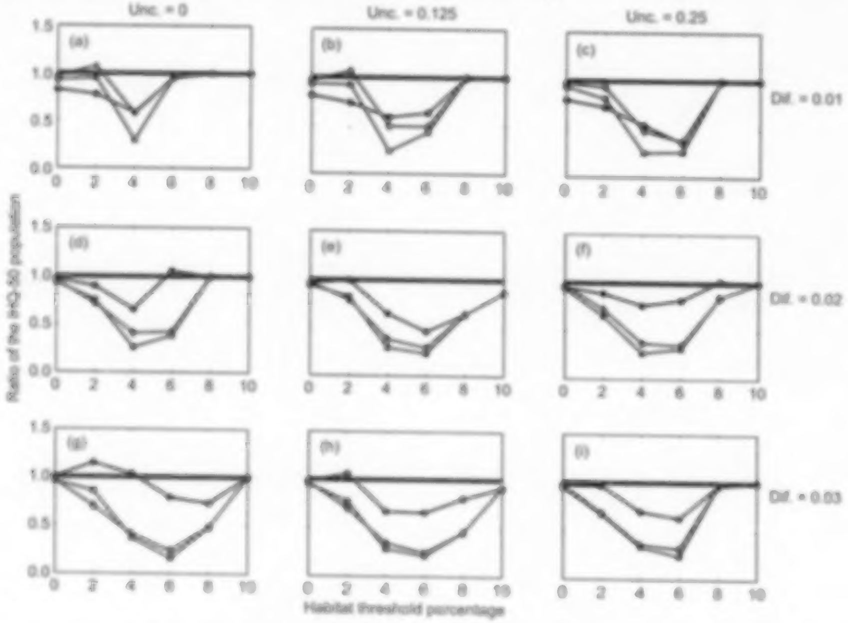
Fig. 6. Mean sessile class 3 population as a ratio of IHQ_50 population. Lines with circles represent the fixed marine protected area (MPA) policy, lines with squares represent the rotating MPA policy, lines with diamonds represent the IHQ_30 policy, and the solid line represents the IHQ_50 policy (Dif., target species diffusion; Unc., uncertainty).



IHQ_50. Both of these policies yield populations that are significantly below the IHQ_50 policy.

For low habitat thresholds ($0\% \le \xi < 6\%$), uncertainty has a negative effect on all the sessile classes and the impact is similar for the different habitat protection policies. This effect is greatest at the 2% habitat threshold. For instance, in the IHQ_50 model, the sessile classes 1, 3, and 5 populations are reduced by 42.98%, 40.97%, and 40.06%, respec-

Fig. 7. Mean sessile class 5 population as a ratio of IHQ_50 population. Lines with circles represent the fixed marine protected area (MPA) policy, lines with squares represent the rotating MPA policy, lines with diamonds represent the IHQ_30 policy, and the solid line represents the IHQ_50 policy (Dif., target species diffusion; Unc., uncertainty).



tively, as uncertainty is increased from 0 to 0.25, assuming a target species diffusion rate of 0.02. Similar reductions result under the IHQ_30 and fixed and rotating MPA policies. For higher habitat thresholds ($6\% \leq \xi \leq 10\%$), the results are mixed and the relative changes are very small. However, the effect of uncertainty on the nontarget populations at the higher habitat thresholds ($6\% \leq \xi \leq 10\%$) is generally greater than that of the target species diffusion rate. The exception to this occurs at the lowest diffusion rate for the fixed MPA model, at which level the fleet size required to catch the TAC is extremely high. Otherwise, higher levels of uncertainty increase both the amount of effort exerted, because of the lower CPUE in the fishery, and the geographical distribution of the fleet. This increases the susceptibility of the nontarget species to both capture and habitat damage.

Although there are few parameter combinations under which the fixed MPA policy yields an equal or higher nontarget species population level, the IHQ_50 generally provides the greatest protection. The situations in which the fixed MPA outperforms the IHQ_50 arise primarily for sessile species that are local recruiters with high habitat thresholds and when there are moderate to high rates of target species diffusion, which limits the increase in effort following implementation of the MPA. For 11 of 56 possible cases, the fixed MPA outperformed the IHQ_50 policy, 6 of which did so by more than 10%. This falls to 5 out of 56 for sessile class 5, one of which exceeds the IHQ_50 population by more than 10% ($d_{\mathrm{Tar}} = 0.03$ and $\sigma = 0$ at the 2% habitat threshold). In general, whenever the fixed MPA outperforms the IHQ_50 at lower habitat thresholds, it does not do so by more than 10%.

For all sessile classes, the rotating MPA always provides less protection than the IHQ_50 policy. However, it does provide more protection than the fixed MPA model whenever the target species diffusion rate is low ($d_{\mathrm{Tar}} = 0.01$). This is the direct result of the fleet size required to execute the TAC under the fixed MPA policy discussed earlier. When compared with the IHQ_30 policy, the rotation MPA only exceeds the populations maintained under the IHQ_30 policy approximately 10% of the time. Otherwise, the IHQ_30 policy yields a slightly higher population than the rotating MPA.

Comparing the conservation of nontarget species with a 50% habitat protection target (IHQ_50) relative to 30% (IHQ_30) unsurprisingly reveals better conservation with the 50% target. However, there are two exceptions that occur at the 2% habitat threshold for sessile classes 2 through 5. This results from a favorable spatial distribution of the fishing effort under these parameter combinations. Recall that IHQ policy only dictates the average habitat quality; it does not indicate where it should be spatially distributed. Also, the spatial distribution of the nontarget species is random and treated as unknown by the fleet. Therefore, favorable conditions at a lower habitat threshold may arise as a result of these compounding effects even though the IHQ_50 policy maintains a higher average habitat quality. However, this improvement is marginal, with nontarget populations never exceeding the IHQ_50 policy by more than 10%.

Discussion

The policy simulations conducted illustrate a number of general findings regarding the relative performance of the four policies simulated and the sensitivity of their performance to both the biological characteristics of the target and nontarget species. We discuss seven general findings that may be drawn from the policy simulations.

General finding one: an individual habitat quota management regime is a more cost-effective means of achieving a given level of average habitat quality than either a fixed or rotating MPA policy

The CPUE results for the four policies simulated indicate that an IHQ management regime is the most cost-effective alternative. The higher CPUE achieved under the IHQ regimes is robust to the target species diffusion, as well as uncertainty, and is not substantially reduced when the habitat target is increased to 50%. In contrast, the cost effectiveness of the fixed MPA is very sensitive to the target species diffusion rate. A diffusion rate of 0.01 lowers the CPUE to around half that obtained at the highest diffusion rate (0.03). This is a direct result of the increase in fleet size required to execute the TAC at the lowest target species diffusion rate. For the IHQ policies, the primary negative impact of raising the habitat target is the substantial increase in the habitat quota price within the fishery. This may increase the probability of noncompliance and require increased spending on enforcement.

General finding two: a conservatively set THQ, IHQ_50, is better suited to the overall protection of a nontarget species than the alternative management regimes for most of the parameterizations of the target and nontarget species

From the simulation results, it is evident that the IHQ_50 management regime provides the most consistent protection for the nontarget species simulated. This is driven by the high average habitat quality maintained under the IHQ policy (50% of the pristine level). For sessile class 1, the IHQ_50 always provided more protection than the rotating MPA and IHQ_30 policies and provided more protection than the fixed MPA policy over 80% of the time. The relative performance of the IHQ_50 policy improved as the degree of global recruitment increased for the sessile nontarget species. For sessile class 5, the IHQ_50 policy outperformed the fixed MPA policy over 90% of the time.

Given the robustness of the IHQ_50 policy to the wide variety of alternative parameterizations modeled and the current lack of knowledge regarding nontarget species characteristics and distributions, it would appear to be both a safer and more efficient habitat protection policy than fixed or rotating MPAs. However, extremely sensitive nontarget species with known spatial distributions may be better protected with fixed MPAs. This discovery is consistent with recent empirical studies (Jennings 2001), but this protection may come at a very high cost to the commercial fleet if the fixed MPA is large and may be counterproductive if the MPA is poorly sited (Kaiser 2005).

General finding three: rotating MPAs are poorly suited to the protection of sessile nontarget species

The rotating MPA policy provides little consistent habitat protection. Although the habitat lying within the MPA increases to a near-pristine level before being reopened, the habitat levels immediately fall as the fleet rushes into the formerly closed MPA to capture the target species that aggregated within. This reduces the habitat within the area from a near-pristine level to a very low level. Although this reduction in habitat quality is temporary, it is still sufficient to wipe out the sessile nontarget species via habitat damage. Consequently, at moderate to high habitat thresholds ($6\% \le \zeta \le 10\%$), the rotating MPA policy yields the complete extinction of the nontarget species by the end of the 70th year simulated. In addition, the average population levels maintained over the duration of the policy are consistently below those of the other three policies simulated. Therefore the cyclical habitat and vessel dynamics that result from the rotating MPA provide inadequate protection for all the sessile classes simulated.

General finding four: high habitat thresholds make it difficult to protect nontarget species regardless of the species' biological characteristics or the attributes of the target species fishery

With moderate to high habitat thresholds, the nontarget populations are already reduced to very low levels before habitat protection is implemented. This depletion occurs regardless of the target species' diffusion rate or the level of uncertainty within the fishery. The depletion may be less extreme if there are areas generally left unfished because of difficulties in fishing these locations, higher costs, or lower productivity (factors we do not model in this paper). However, this result underscores the importance of implementing habitat protection early.

Even once protection is implemented, maintaining populations of extremely sensitive nontarget species is difficult. A MPA is capable of protecting the population that resides within it, but it will concentrate effort in the fishing grounds that remain open, thereby further exacerbating the habitat problem in those areas. Increasing the size of the closed areas may increase the protection of habitat-dependent species if it is correctly located, but it may substantially increase harvest costs. Furthermore, it is likely to exacerbate the damage in the area left open, increasing the risk to any habitat-dependent species that are not protected by the MPA. Although the IHQ system provides a more broadly distributed protection, which may be critical when species distributions are unknown, it does not guarantee protection in any location.

General finding five: the degree of global versus local recruitment possessed by the sessile nontarget species influences the relative performance of the policies

The degree of global versus local recruitment exhibited by the nontarget species influences their ability to resettle in areas that were previously damaged by fishing. The purely local recruiting species, sessile class 1, is incapable of resettling an area from which they have been eliminated because of a reduction in habitat quality, even if the habitat regenerates. Therefore, a policy that provides spatially consistent habitat protection is more desirable for these organisms. The fixed MPA provides this protection for 20% of the fishery and performs better than the IHQ_50 for this class of sessile organisms at the higher habitat thresholds. This results because only a near-pristine area is capable of maintaining the population at these habitat thresholds. However, because the fixed MPA severely reduces the habitat outside of the MPA, it generally results in the elimination of any habitat-dependent species located outside of the MPA.

For the sessile classes with a higher degree of global recruitment, sessile classes 4 and 5, the IHQ_50 performs better than the fixed MPA. This result is driven by the habitat dynamics under the IHQ_50 policy. Habitat under the IHQ_50 policy maintains a fairly consistent and diffuse array of areas with high habitat quality. These areas may be fished and the habitat reduced if the target population becomes highly concentrated in them, but if the nontarget species exhibits some degree of global recruitment, these areas may be resettled once habitat regenerates. This finding indicates that at higher habitat thresholds, a locally recruiting species may be better protected by a fixed MPA, whereas globally recruiting species do better under the IHQ_50 policy.

General finding six: the greater the target species diffusion, the greater is the ability of both fixed and rotating MPAs to protect the sessile nontarget species

Diffusion has a pronounced effect on the performance of fixed and rotating MPAs. With fixed MPAs, a low diffusion rate dramatically decreases the ability of the fixed MPA to protect the nontarget species. This results from the rapid increase in the fleet size required to capture the TAC as the target species becomes concentrated inside the MPA with little spillover into the fishing grounds. This increase in fleet size and total effort dramatically reduces the habitat level outside of the MPA and causes the nontarget species to be virtually eliminated outside the MPA. At higher diffusion rates, this does not occur because the required fleet size is significantly smaller.

For the rotating MPA, a similar phenomenon occurs but is temporally dynamic. The fleet concentrates all of its effort in recently opened MPAs because the low diffusion target species concentrates within the MPA before its being opened. This intense effort within the former MPA causes the habitat to substantially deteriorate and eliminates the nontarget species. At higher diffusion rates, the target species becomes less temporally concentrated within the MPA. This reduces the concentration of effort in reopened areas and increases the probability that habitat quality in some locations remain above the level required to sustain the nontarget species. These fleet dynamics, both temporal and spatial, highlight the importance of modeling the fleet's behavior. The success of any management instrument, whether MPAs or IHQs, will hinge on the economic decisions made by fishers across time and space (Smith and Wilen 2003; Kaiser 2005).

General finding seven: higher degrees of uncertainty in the target species distribution decrease the ability of all policies to protect the nontarget species

A higher degree of uncertainty causes the amount of pristine habitat within the fishery to be reduced because effort is more evenly spread out. For the IHQ regime, it results in fishing areas that would otherwise have remained completely unfished. For instance, as uncertainty increases from 0 to 0.25, holding diffusion at 0.01, the percentage of pristine habitat maintained over the last 20 years of the simulation decreases from 13.52% to 9.26% for IHQ_30 model and from 43.71% to 40.23% for IHQ_50. For the MPAs, uncertainty reduces the tendency of vessels to concentrate on the periphery of the closed area. This spreading-out of the habitat damage increases the probability that the habitat in a region will not meet the habitat threshold specified for the nontarget species.

Overall, these simulations suggest that an IHQ system, with a conservative habitat target "stock" level of 50%, is a cost-effective management instrument, generally capable of mitigating the effects of commercial fishing on sessile nontarget species more effectively than either fixed or rotating MPAs. Although fixed MPAs will provide more certain protection if they are located correctly (Kaiser 2005), this may not be possible or cost effective when the distributions of the nontarget species are unknown or widely distributed. An IHQ system does not preclude the simultaneous use of MPAs, which might be used to provide protection for locations known to contain critically threatened species.

We have assumed a homogeneous habitat type within our simulated fishery and expect that it may be important to ensure some level of protection for all types of habitat present. This could be achieved by mapping the spatial distribution of alternative habitat types and creating separate habitat quotas and targets to manage each type of habitat. This should also improve the performance of the IHQ regime at protecting a broader range of habitat-dependent species if their distributions are correlated with the separate habitat types identified and regulated.

An IHQ system may force fishers to incur a substantial up-front cost to implement the management regime. However, given the cost savings achieved relative to the alternative management regimes, the IHQ regime may still be preferable. There will invariably be some objections voiced by fishers as the IHQ system will require high-resolution tracking of their activities and all fishers would be aware of where others are fishing (though they could not identify which vessels are fishing where or how much they are catching). However, achieving the sufficient protection of benthic habitat, as well as its constituent nontarget species, is likely to require a compromise between privacy and preserving fishers' freedom to choose where and when to fish.

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Depth-specific patterns in benthic–planktonic food web relationships in Lake Superior

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Abstract: In an investigation of the spatial characteristics of Laurentian Great Lakes food webs, we examined the trophic relationship between benthic amphipods (*Diporeia*) and plankton in Lake Superior. We analyzed the carbon and nitrogen stable isotope ratios of *Diporeia* and plankton at stations in water column depths of 4–300 m. Neither $\delta^{15}N$ nor $\delta^{13}C$ of plankton from the upper 50 m of the water column varied significantly with station depth. *Diporeia* isotope ratios exhibited depth-specific patterns reflecting changes in food sources and food web relationships with plankton. *Diporeia* was ^{13}C enriched at station depths of <40 m, reflecting increased dietary importance of benthic algae. There was a systematic increase in *Diporeia* $\delta^{15}N$ with depth, which appeared to result from a combination of dietary shifts in the nearshore and decompositional changes in *Diporeia*'s principal food, sedimented plankton, in deep habitats. *Diporeia* $\delta^{13}C$ and $\delta^{15}N$ together described changes in food web isotope baseline with depth. They also discriminated three depth strata representing photic, mid-depth, and profundal zones. These findings have implications for our understanding of Great Lakes food webs and analyses of trophic position within them, the ecology of zoobenthos and plankton communities, and sampling designs for large lakes.

Résumé : Au cours d'une étude des caractéristiques spatiales des réseaux alimentaires des Grands Lacs laurentiens, nous avons analysé les relations trophiques entre les amphipodes benthiques (*Diporeia*) et le plancton au lac Supérieur. Nous avons déterminé les rapports d'isotopes stables de carbone et d'azote chez *Diporeia* et dans le plancton dans des stations dont la profondeur de la colonne d'eau variait de 4 m à 300 m. Ni le $\delta^{15}N$, ni le $\delta^{13}C$ du plancton des 50 m supérieurs de la colonne d'eau ne varient significativement en fonction de la profondeur de la station. Chez *Diporeia*, les rapports isotopiques forment des patrons spécifiques en fonction de la profondeur, ce qui indique des changements dans les sources de nourriture et les relations avec le plancton dans le réseau alimentaire. Il y a un enrichissement en ^{13}C chez *Diporeia* aux stations <40 m, ce qui signale une importance accrue des algues benthiques dans le régime alimentaire. Il y a une augmentation systématique de $\delta^{15}N$ chez *Diporeia* en fonction de la profondeur, qui semble résulter d'une combinaison d'un changement de régime près du rivage et de modifications dans la décomposition du plancton en sédimentation, la nourriture principale de *Diporeia*, dans les habitats plus profonds. Ensemble $\delta^{13}C$ et $\delta^{15}N$ permettent de décrire les changements dans la ligne de base isotopique du réseau alimentaire en fonction de la profondeur. Ils permettent aussi de distinguer trois strates de profondeurs qui représentent les zones photique, intermédiaire et profonde. Ces résultats affectent notre connaissance des réseaux alimentaires dans les Grands Lacs, les déterminations des positions trophiques dans ces réseaux, l'écologie des communautés de zoobenthos et de plancton et l'élaboration de plans d'échantillonnage dans les lacs de grande taille.

[Traduit par la Rédaction]

Introduction

A leading challenge in understanding and managing large lakes lies in comprehending their spatial complexity. Aquatic habitat and resource heterogeneity have been linked to the diversity and productivity of communities (e.g., Eadie and Keast 1984; Benson and Magnuson 1992; Pratt and Smokorowski 2003), and interaction among aquatic habitats is recognized as a critical process in the function of whole-lake food webs (Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002). One way to address this issue is through spatially explicit models of aquatic production (e.g., Brandt et al. 1992; Mason et al. 1994) that incorporate heterogeneity in physical habitat quality to obtain more realistic scenarios than those that consider the average state of whole systems. Other research and management efforts could similarly be improved by including characteristics of spatial pattern. If large systems are divisible into physically or functionally distinct habitats according to properties such as productivity, biological communities, or food web relationships, then management goals and monitoring designs could be adjusted appropriately.

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In Lake Superior of the Laurentian Great Lakes, improved comprehension of food web spatial relationships would help us to better understand and manage the system. The Lake Superior fish community is structured by depth, with nearshore fishes (e.g., "lean" lake trout (*Salvelinus namaycush*), rainbow smelt (*Osmerus mordax*), lake herring (*Coregonus artedi*), and slimy sculpin (*Cottus cognatus*)) giving way to a deepwater assemblage typified by "siscowet" lake trout (*Salvelinus namaycush siscowet*), bloater (*Coregonus hoyi*), kiyi (*C. kiyi*), and deepwater sculpin (*Myxocephalus thompsoni*). Recent investigations have explored differences and potential interaction between nearshore and deepwater trophic pathways (Harvey and Kitchell 2000; Kitchell et al. 2000; Harvey et al. 2003). However, the ultimate energetic base of nearshore and deepwater production, and therefore the productive capacity of those pathways, remains unresolved. An investigation of the trophic relationships among primary consumers would help to provide that information, as well as information on the ecology of a key trophic level. Further, because stable isotope techniques are used to trace food web pathways, improved knowledge of depth-specific patterns in the isotope signatures of organisms at the base of the food web would help to clarify the interpretation of stable isotope data.

A number of previous efforts have attempted to partition Lake Superior into regions based on physical, chemical, and biological characteristics. Divisions based on temperature (Upper Lakes Reference Group 1977), benthic communities (Cook 1975; Dermott 1978), and phytoplankton biomass and taxonomy (Munawar and Munawar 1978) have included water column depth as a key parameter. Johnson et al. (2005) defined three western Lake Superior regions based on bathymetry and other limnological characteristics and found differences in the fish and zooplankton assemblages among those regions. As a further step toward understanding the spatial ecology of the Great Lakes, we are exploring food web characteristics as an ecological basis for defining habitat classes. Here we describe depth-specific patterns in the carbon and nitrogen stable isotope signatures of zoobenthos and plankton. These patterns, which reflect variations in resource use and food web relationships, have implications for our understanding of Great Lakes food webs, the ecology of benthic and planktonic communities, and sampling designs for large lakes.

Materials and methods

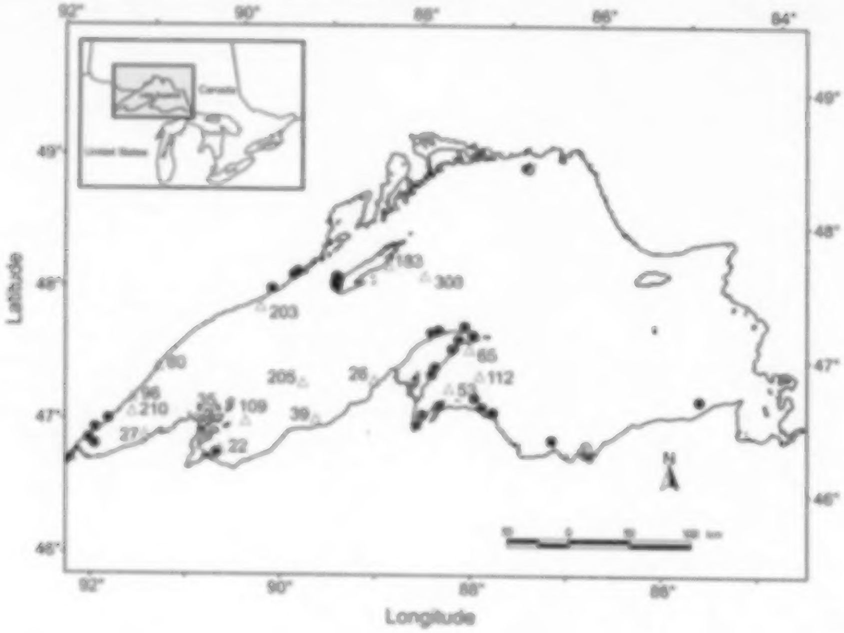
We sampled food web components at an array of shallow and deepwater stations in western Lake Superior in 1997 and 2001 and at an intensive set of nearshore stations in 2001, 2002, and 2003 (Fig. 1). These efforts reflect a progression from early explorations to more detailed analyses. The 1997 and 2001 samples were taken during September "Circle Cruises" circumnavigating western Lake Superior in an ongoing effort to evaluate coastal zones and the major subbasins of western Lake Superior. Station depths ranged from 22 to 300 m. The nearshore effort (2001, 2002, and 2003) included stations from depths of 4–166 m and encompassed a variety of nearshore habitats, including open shorelines, bays, and areas near tributaries (Fig. 1). Nearshore sampling took place in mid- to late summer (July – early September).

Plankton samples were collected using 50 m vertical (offshore) or horizontal (nearshore) tows with a 0.5 m diameter, 80 μm mesh plankton net. Zoobenthos were collected using PONAR grabs. Our analyses of zoobenthos focus on the amphipod *Diporeia* spp., which is the dominant organism in the Lake Superior benthic community in both abundance and biomass (Cook 1975; Dermott 1978; Scharold et al. 2005). In 1997, single plankton and *Diporeia* samples were collected at each station, and plankton retained on a 183 μm sieve were analyzed. In 2001, triplicate plankton and zoobenthos samples were usually taken, but because of low *Diporeia* abundance at the deepest stations, some samples contained too few *Diporeia* for analysis and only single or duplicate samples were analyzed. In 2001, we divided plankton samples into two size fractions (110–253 μm and >253 μm) using Nitex sieves and identified the contents of each size fraction microscopically. Each benthic grab sample was placed into an elutriation device and washed through a 500 μm mesh Nitex sleeve. The amphipods were picked from the retained material under a dissecting scope. All samples were immediately rinsed with 1 mol·L^{-1} HCl and deionized water and frozen pending analysis.

In the nearshore, a total of 125 stations at 28 nearshore sites were sampled for zoobenthos and plankton (Fig. 1). At each nearshore site, sampling stations were located along one or two transects established perpendicular to the shoreline. One transect was normally used, but for sites located near tributaries, two transects (one at the tributary mouth and one 1–2 km away) were established to include a range of habitat characteristics. Plankton and zoobenthos samples were taken along each transect from approximately 5, 10, 20, and >30 m depth stations. Zoobenthos were primarily *Diporeia*, although samples from depths of <10 m occasionally also included the amphipods *Gammarus* and *Hyalella*. All amphipods captured on Circle Cruises were *Diporeia*. Taxonomic analyses of 2001 nearshore samples revealed that in 47 (i.e., 94%) of the 51 stations sampled, more than 98% of the amphipods present were *Diporeia*. *Gammarus* and *Hyallela* constituted 25% of the amphipods at one station and >50% at the two remaining stations. All amphipods were included in our analyses. Because *Gammarus* and *Hyalella* were infrequently encountered, and because the trends in our data extend beyond the depths inhabited by them, we believe our results to be independent of amphipod taxonomy and discuss our results with respect to *Diporeia* alone.

Diporeia lipid content, and therefore $\delta^{13}C$, might be affected by body size (Guiguer and Barton 2002). We therefore sorted amphipods collected in 2001 into three size categories before analysis (<3.6 mm, 3.6–5.4 mm, and >5.4 mm). Lipids were not extracted from *Diporeia* before stable isotope analysis. In a separate study, with different size categories of *Diporeia* available, extraction of lipids from three size classes of Lake Superior *Diporeia* (3.8–4.7 mm, 4.7–6.6 mm, and 6.6–7.6 mm) significantly increased $\delta^{13}C$ by approximately 4‰ (analysis of variance, $p < 0.001$). There were no significant differences among size categories in the $\delta^{13}C$ shift after extraction. Lipid extraction had no significant effect on *Diporeia* $\delta^{15}N$ (G.S.Peterson, unpublished data). We analyzed the samples for carbon and nitrogen isotopes on a Micromass Isochrom-EA NC2500

Fig. 1. Outline of Lake Superior with locations of Circle Cruise sampling stations (with depths in metres; open triangles) and nearshore sampling sites (solid circles). Inset shows location in the Great Lakes region.



isotope ratio mass spectrometer (GV Instruments, Manchester, UK). Isotope ratios are expressed as δ values, parts-per-thousand deviations from the ratios found in reference materials (Peedee belemnite C and atmospheric N). Samples enriched with the heavier isotope (^{13}C or ^{15}N) have δ values that are relatively more positive.

We performed statistical analyses using software packages. We used SYSTAT (Systat Software Inc. 1998) to test distributional assumptions, for *t* tests, analyses of variance (ANOVA), and multivariate analyses of variance (MANOVA), and to generate semivariograms to test for spatial autocorrelation among samples. Semivariograms of spatially ordered data revealed no evidence of spatial autocorrelation among stations. Dissimilarity of isotope values did not increase with increasing distance between samples and, in fact, showed no pattern, supporting assumptions of sample independence. We used SigmaPlot 2004 for Windows (Systat Software Inc. 2004) to generate and test linear and nonlinear regressions describing patterns in δ^{15}N and δ^{13}C with depth.

Results

Samples from the Circle Cruises showed a marked increase in *Diporeia* δ^{15}N with station depth (Fig. 2*a*) and ^{13}C enrichment of *Diporeia* in nearshore waters (Fig. 2*b*). There were no significant differences in the δ^{13}C or δ^{15}N of different *Diporeia* size classes from the 2001 sampling; we therefore pooled all size categories from each station. The difference in amphipod δ^{15}N between the shallowest and deepest stations was approximately 4‰, which is greater than the ^{15}N enrichment generally observed between adjacent trophic levels (DeNiro and Epstein 1981; Vander Zanden and Rasmussen 2001).

Neither δ^{15}N nor δ^{13}C of Circle Cruise plankton from the upper 50 m water column varied with station depth. The small (110–253 μm) size fraction from 2001 is plotted (Fig. 2); larger size fractions (>183 μm in 1997, >253 μm in 2001) followed similar patterns as the data plotted, except that δ^{15}N means and standard deviations were greater (mean (standard deviation, SD) δ^{15}N = 3.0‰ (1.2‰) for 1997 plankton, –1.3‰ (0.6‰) for 2001 small size fractions and 1.1‰ (1.3‰) for 2001 large fractions; mean (SD) δ^{13}C was –28.7‰ (1.2‰) for 1997 plankton, –26.9‰ (1.3‰) for 2001 small fractions and –28.2‰ (1.2‰) for 2001 large fractions). 2001 Circle Cruise plankton samples were dominated by *Holopedium*, *Bythotrephes*, *Daphnia*, and diaptomid copepods. Smaller size fractions contained a mixture of rotifers, nauplii, and diatoms. *Mysis* were also occasionally captured, although few are in the water column during daylight hours. We pooled 1997 and 2001 *Mysis* samples for data analyses: δ^{15}N mean (SD) = 4.4‰ (1.1‰); δ^{13}C mean (SD) = –26.4‰ (1.4‰). Like plankton, their primary food, the δ^{15}N of *Mysis* was invariant with depth (linear regression, $F_{[1,7]} = 0.09$, $P = 0.77$, $N = 9$), as was *Mysis* δ^{13}C (linear regression, $F_{[1,6]} = 0.19$, $P = 0.68$, $N = 7$).

Studies in 2001, 2002, and 2003 focusing on nearshore regions of Lake Superior showed that *Diporeia* δ^{15}N values ranged from approximately –2‰ to 2‰ in the shallowest stations and then increased to approximately 5‰ at 160 m (Fig. 3*a*). The systematic increase in δ^{15}N with depth for combined 1997 and 2001 Circle Cruise and nearshore *Diporeia* samples was described by the equation $\delta^{15}\text{N} = -2.79 + 1.44\ \ln(\text{depth})$. The regression was significant ($R^2 = 0.6$, $F_{[1,144]} = 273$, $P < 0.0001$). δ^{15}N values of neither plankton

Fig. 2. (*a*) δ^{15}N and (*b*) δ^{13}C of 1997 Circle Cruise *Diporeia* (solid circles), 2001 Circle Cruise *Diporeia* (open circles), and 2001 Circle Cruise plankton, 110–253 µm size fraction (inverted solid triangles) versus water column depth at sampling station. Vertical lines show ±1 SD.

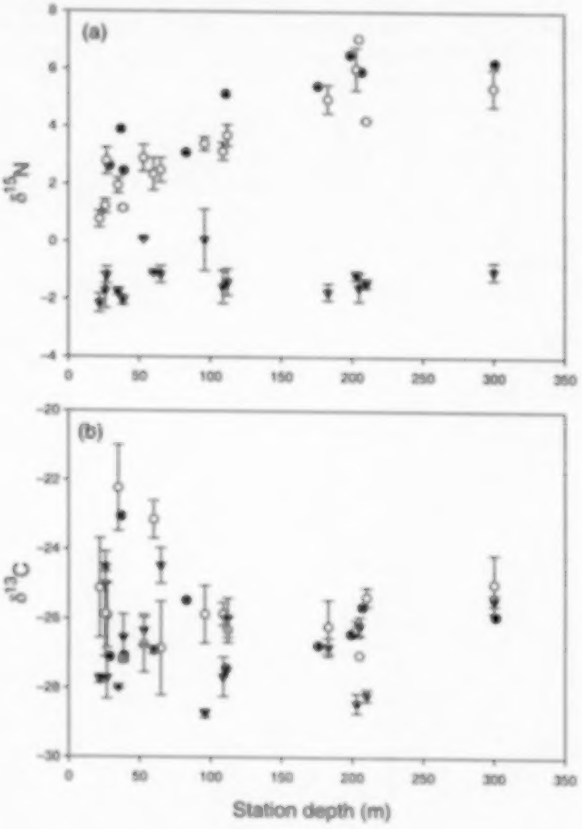
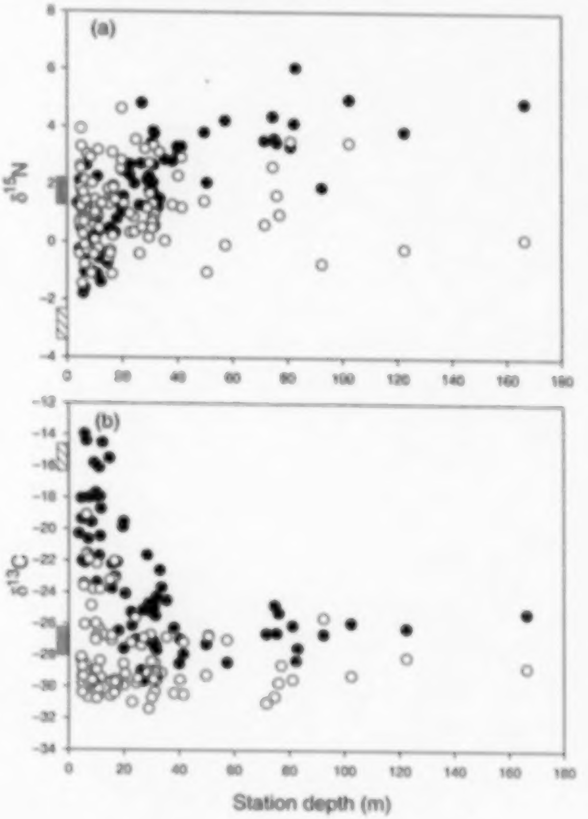


Fig. 3. (*a*) δ^{15}N and (*b*) δ^{13}C of *Diporeia* (solid circles) and plankton (open circles), from nearshore sampling effort (2001–2003), versus water column depth at sampling station. Also shown are ranges of isotope ratios for benthic algae (hatched bars on *y* axis; data from Strand 2005) and phytoplankton (cross-hatched bars on *y* axis; data from Pang and Nriagu (1977) and Keough et al. (1996)) from Lake Superior.



size fraction varied with depth of the water column. The two size fractions of plankton had significantly different δ^{15}N values (mean δ^{15}N of small fraction = 1.2‰; δ^{15}N of large size fraction = 2.7‰; paired *t* test, $t = 11.261$, $P < 0.001$, $N = 95$). Differences in nitrogen ratios of the two size fractions probably reflected trophic-level differences stemming from the presence of algae in the small fraction and carnivorous zooplankton (e.g., *Bythotrephes*) in the larger fraction. *Diporeia* δ^{13}C values were as high as −14‰ in the shallowest stations and then became progressively ^{13}C-depleted to a depth of ~40 m (Fig. 3*b*). The decline in *Diporeia* δ^{13}C values from the shallowest stations to depths of 40 m for combined 1997 and 2001 Circle Cruise and nearshore samples was described by the equation δ^{13}C = −17.78 − 0.25(depth) ($R^2 = 0.50$, $F_{[1,84]} = 83.5$, $P < 0.0001$). Beyond 40 m, *Diporeia* δ^{13}C remained essentially constant. Plankton carbon ratios generally ranged from −26‰ to −31‰, except that 13 nearshore samples were ^{13}C-enriched to values above −26‰ (Fig. 3*b*). The δ^{13}C of the two size fractions of plankton were not significantly different (mean δ^{13}C of small fraction = −28.2‰; mean δ^{13}C of large fraction = −28.1‰; paired *t* test, $t = 0.693$, $P = 0.49$, $N = 95$).

Discussion

Sedimented phytoplankton are generally considered to be the major food for *Diporeia* in the Great Lakes (Dermott and Corning 1988; Gardner et al. 1990; Fitzgerald and Gardner 1993). However, the nearshore elevation of *Diporeia* carbon ratios indicates the influence of ^{13}C-enriched food sources in shallow water. Increased importance of benthic algae to *Diporeia* diets in the littoral zone would explain this pattern, as benthic algae and consumers relying on benthically fixed carbon are generally ^{13}C-enriched compared with phytoplankton- and plankton-based food webs (France 1995; Hecky and Hesslein 1995). The decline in *Diporeia* δ^{13}C values from inshore to 40 m would be expected with a dietary progression from mostly benthic algae inshore to mostly sedimented phytoplankton at depths ≥40 m. Lake Superior epilithic algae had δ^{13}C values ranging from −14.7‰ to −17.3‰ (Strand 2005); Lake Superior phytoplankton had δ^{13}C values from −26.3‰ to −27.9‰ (Keough et al. 1996), and nearshore 80 to 253 µm plankton δ^{13}C mean (SD) = −28.2‰

(2.5‰) (this study). Benthic algae are available in the nearshore photic zone in Lake Superior, which extends to a depth of 25–50 m (Schertzer et al. 1978; Johnson et al. 2005), and have been observed to grow in thick mats in some areas (Edsall et al. 1991). Guiguer and Barton (2002) found ^{13}C enrichment of *Diporeia* at 30 m, but not at 50 m, in Georgian Bay, Lake Huron, during the summer growing season and attributed it to consumption of benthic algae in the littoral zone. Because we did not extract lipids, which tend to be ^{13}C-depleted (Tieszen et al. 1983; Guiguer and Barton 2002), from our samples, some of the variability in $\delta^{13}C$ with depth may be due to variations in lipid content with depth. However, the increase in *Diporeia* $\delta^{13}C$ after lipid extraction ranges from 2‰ (Guiguer and Barton 2002) to 4‰ (G.S. Peterson, unpublished data), whereas the depth-specific change in $\delta^{13}C$ in our nearshore samples is as great as 14‰. We suggest that ingestion of benthic algal carbon is primarily responsible for the increase in nearshore *Diporeia* $\delta^{13}C$, which is detectable to a depth of about 40 m. The trends observed for *Diporeia* were unlike those reported for chironomid larvae, which had higher $\delta^{13}C$ and $\delta^{15}N$ values with depth in eutrophic lakes, because of increased incorporation of methanotrophic bacteria (Grey et al. 2004*a*, 2004*b*).

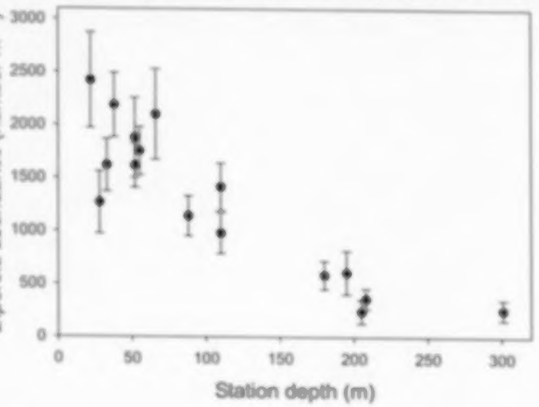
Patterns in nitrogen isotope data also support the idea that benthic algae contribute significantly to nearshore *Diporeia* diets. *Diporeia* $\delta^{15}N$ values at shallow stations were as low as –2‰, which is near the lower limit of measured $\delta^{15}N$ values for Lake Superior plankton (Pang and Nriagu 1977; Keough et al. 1996; this study). In contrast, epilithic algae from the Lake Superior littoral zone have measured $\delta^{15}N$ values of –3.3‰ to –1.6‰ (Strand 2005); ingestion of benthic algae by nearshore *Diporeia* would thus explain the observed nitrogen isotope patterns. As with the carbon data, ^{15}N enrichment of *Diporeia* with depth through the littoral zone may reflect a gradual dietary shift away from the influence of benthic algae to a more homogeneous diet of sedimented phytoplankton.

The continued ^{15}N enrichment of *Diporeia* to a maximum $\delta^{15}N$ of ~6‰ at deep stations is consistent with trends expected from the decomposition of phytoplankton during sedimentation. The processes of particle decomposition, nitrogen release, and the associated dynamics in dissolved and particulate nitrogen isotope ratios have been described with regard to the cycling and vertical transport of nitrogen in the ocean (Saino and Hattori 1980, 1985; Altabet 1988) and in the Great Lakes (Ostrom et al. 1998; McCusker et al. 1999) and are relevant to our results. As detrital plankton settles through the water column and decomposes, the lighter N isotope is preferentially released, and the residual detritus becomes progressively ^{15}N-enriched as it sinks (Saino and Hattori 1980; Altabet 1988; Ostrom et al. 1998). The increases in detrital $\delta^{15}N$ apparently stem from a combination of microzooplankton grazing and nitrogen remineralization, protein hydrolysis, and losses of dissolved organic nitrogen from bacteria and phytoplankton (Checkley and Miller 1989; Silfer et al. 1992; Hoch et al. 1996). It follows that zoobenthos that feed upon that sedimented detritus should become similarly ^{15}N-enriched, progressively so with depth. Ostrom et al. (1998) found that the $\delta^{15}N$ of Lake Superior sediments increased from 3.3‰ at 120 m to 5.3‰ at 400 m and that the $\delta^{15}N$ of the benthic nepheloid layer (BNL) at those depths increased from 1.7‰ to 3.3‰. *Diporeia* $\delta^{15}N$ values predicted from our combined sample regression are 4.1‰ at 120 m and 5.8‰ at 400 m, which would represent 0.8‰ and 0.5‰ ^{15}N enrichment over sediments and 2.4‰ and 2.5‰ ^{15}N enrichment over the BNL, respectively. The latter values compare well with measured N-fractionation estimates of 2.52‰ ± 2.5‰ for freshwater herbivores (Vander Zanden and Rasmussen 2001). The marine amphipods *Parhyale hawaiensis* and *Amphithoe valida* had N-fractionation values of 2.2‰ to 2.7‰ and –0.1‰ to –0.7‰ compared with their diets, respectively (Macko et al. 1982).

Beyond 40 m depth, $\delta^{13}C$ of *Diporeia* was relatively constant. Meyers and Eadie (1993) found a 1‰ ^{13}C enrichment in particles sinking to depths of 140–166 m in Lake Michigan, which may reflect isotopic enrichment during particle sedimentation, as with nitrogen isotopes. Nitrogen appears to be more rapidly lost than carbon during particle decomposition, and ^{15}N enrichment with depth is therefore more dramatic than ^{13}C enrichment (Saino and Hattori 1980). The relatively consistent $\delta^{13}C$ values of plankton collected from the well-mixed upper water column throughout western Lake Superior were expected. However, some nearshore plankton samples had elevated $\delta^{13}C$ values, which could have been caused either by a ^{13}C-enriched inorganic carbon source for plankton or by inclusion of suspended ^{13}C-enriched benthic algae in the wave-swept shallow nearshore. Although we did not analyze the taxonomic composition of these samples, we found sand in some of the ^{13}C-enriched shallow nearshore samples, but not in their counterparts in the deeper nearshore (M.E. Sierszen, personal observation), indicating the potential for benthic material to have influenced the nature of inshore samples.

The spatial patterns that we see in stable isotope ratios reflect biogeochemical processes that influence the ecology of important primary consumers in large lakes. Our data indicate that in the nearshore photic zone, benthic algae contribute to the diet of *Diporeia*. Sedimented phytoplankton then appear to become especially important to *Diporeia* beyond the photic zone, where *Diporeia* population peaks occur. In western Lake Superior, *Diporeia* obtains highest populations in depths from approximately 40–70 m (Fig. 4, plotted from data in Scharold et al. 2005). The abundances of *Diporeia* and other benthic taxa in Lake Superior decrease beyond depths of 70 m, with midlake profundal regions very sparsely populated (Cook 1975; Dermott 1978; Auer and Kahn 2005). Reduced food quality has been cited as a possible reason for offshore declines in *Diporeia* abundance in Lake Michigan (Evans et al. 1990) and for zoobenthos in general in Lake Superior (Mozley and Howmiller 1977). Decomposition of phytoplankton as it sinks through the water column may result in reduced nutritional quality of detritus reaching deep sediments. An estimated 96% of the organic carbon produced in the photic zone of Lake Michigan is recycled before it sinks 100 m (Eadie et al. 1984). Although sediments in the deep depositional basins of Lake Superior have higher organic C contents than those in shallower areas (Thomas and Dell 1978), much of the organic matter in profundal Great Lakes sediments is refractory (Kemp 1969). In deepwater habitats, therefore, decomposition of sinking particles may limit benthic food resources and the organisms that depend on them. This may partly explain the habits of *Mysis*

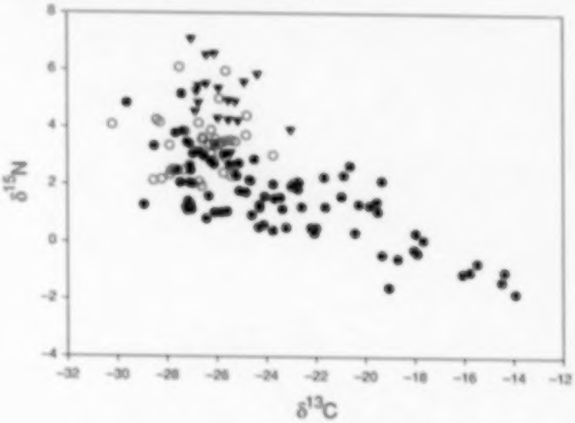
Fig. 4. Abundance (animals·m^{-2}, mean ± SD) of *Diporeia* versus depth at 16 stations in western Lake Superior, averaged over 7 years of monitoring (1994–2000) (from Scharold et al. 2005).



relicta, a major component of the Great Lakes invertebrate community and, like *Diporeia*, an important food for many Great Lakes fishes (Foltz and Norden 1977; Janssen and Brandt 1980; Conner et al. 1993). Unlike *Diporeia*, *Mysis* increases in abundance with depth in the Great Lakes and remains abundant to depths of at least 200 m (Sell 1982; Johannsson 1995; Pothoven et al. 2004). *Mysis* is epibenthic during the day and will feed upon *Diporeia* (Parker 1980; Johannsson et al. 2001), but it obtains most of its nutrition feeding upon living plankton during its diel vertical migrations (Bowers and Grossnickle 1978; Bowers and Vanderploeg 1982; Johannsson et al. 2001). The strategy of relying on water column resources instead of nutritionally poor detritus may allow *Mysis* to thrive in profundal zones where relatively sedentary zoobenthos are less successful.

Studies of benthic–pelagic coupling have demonstrated the interplay between benthic and water column habitats and the significance of their contributions to whole systems. Even in large lakes, littoral zone benthic production is important to whole-lake food webs (Hobson and Welch 1995; Vadeboncoeur and Steinman 2002; Vadeboncoeur et al. 2002). At the same time, deposition of detrital phytoplankton provides a substantial amount of the energetic resources for zoobenthos in deep lakes (Johnson and Wiederholm 1992; Goedkoop and Johnson 1996). Our results reveal a finer scale to these linkages, with depth-specific patterns in the relationship between zoobenthos and plankton. Because these patterns can provide insight into ecological relationships across depth strata, they may be valuable to consider when designing sampling strategies. Sampling classes that target the littoral photic zone, the mid-depth zone of strong plankton–benthos coupling, and profundal areas may capture ecologically relevant characteristics of large lakes. A plot of the δ^{15}N versus δ^{13}C of all *Diporeia* samples, separated into three depth categories that might reasonably represent those three zones (<40 m, 40–150 m, >150 m), captures the overall response in *Diporeia*'s isotopic signature with depth (Fig. 5). The plot shows that the entire range of δ^{13}C values is spanned within the 0–40 m zone, and that beyond the depth of 40 m, most of the isotope variability is along the δ^{15}N axis. We tested for significant differences among the three depth categories using MANOVA with δ^{13}C and δ^{15}N as dependent variables. To meet normal distribution and equal variance requirements for MANOVA, we made all data positive and reciprocally transformed the δ^{13}C data (i.e., $1/(\delta^{13}C + 32)$; $\delta^{15}N + 2$). Data from the three depth categories form three statistically distinct groups along the plot (MANOVA, Wilks' $\lambda = 0.40$, $F_{[4,268]} = 38.7$, $P < 0.001$; for each between-group contrast, Wilks' $\lambda \le 0.73$, $F \ge 24.6$, $P < 0.001$). This suggests that food web attributes, characterized by stable isotope analysis, may be useful to define ecological habitats in large systems.

Fig. 5. δ^{15}N of all *Diporeia* samples plotted against δ^{13}C by three depth categories: <40 m, solid circles; 40 to 150 m, open circles; >150 m, inverted solid triangles.



The trophic position of consumers can be calculated from the δ^{15}N of those consumers relative to the δ^{15}N of representative organisms at or near the food web base (Cabana and Rasmussen 1996). Variations in the isotope signatures of baseline organisms and, in particular, ^{15}N enrichment of profundal benthos have been examined as important factors to consider when calculating consumer trophic position (Vander Zanden and Rasmussen 1999; Post 2002). Vander Zanden and Rasmussen (1999) presented a δ^{15}N versus δ^{13}C plot, similar to our Fig. 5, for primary consumers (littoral benthos, zooplankton, and profundal benthos) in eastern Canadian lakes, which reflected the food web isotopic baseline across those lakes. Our isotopic baseline similarly exhibits a negative relationship between δ^{15}N and δ^{13}C, mediated by depth. The overall δ^{15}N–δ^{13}C relationship for *Diporeia* was highly significant and described by the exponential decay function $\delta^{15}N = 7.56 \exp[-1.08(\delta^{13}C)]$ ($R^2 = 0.40$, $F_{[1,144]} = 96.6$, $P < 0.0001$, $N = 145$; $\exp(x) = e^x$). Although a logistic relationship might better represent the upper and lower limits to isotope fractionation in natural systems, the exponential function reflects the response of our data within the measured range. These results are similar to those of Vander Zanden and Rasmussen (1999) in response and application but are specific to the dominant benthic primary consumer in western Lake Superior. Similar analyses that include additional taxa in Lake Superior and other Great Lakes may ultimately provide a generalized baseline response. An understanding of the processes underlying depth-specific patterns in isotope signatures, and descriptions of those patterns, should be especially valuable to researchers undertaking stable isotope food web investigations in marine systems and the world's Great Lakes.

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Recovery from acidification in Nova Scotia: temporal trends and critical loads for 20 headwater lakes

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Abstract: The chemical response of 20 headwater lakes in Nova Scotia to reduced acid deposition was investigated using trend analysis, and the need for further reductions was assessed using two steady-state, critical load models. Significant decreases were observed in the concentration of nonmarine sulphate (SO_4^{2-}) and hydrogen (H^+) at four wet deposition monitoring stations across Atlantic Canada since 1984. Dominant trends in surface water were decreasing SO_4^{2-} concentrations, with little improvement in alkalinity and H^+. Based on the Steady State Water Chemistry (SSWC) and First-order Acidity Balance (FAB) models, and using a critical chemical limit for acid-neutralizing capacity of 20 $\mu mol_c \cdot L^{-1}$, critical load is exceeded at 9 and 13 of the 20 study lakes, respectively. Application of the SSWC model suggests that sulphur (S) deposition must be reduced by 37.3 $mmol_c \cdot m^{-2} \cdot year^{-1}$ from 1997 levels to prevent critical load exceedance at 95% of the study lakes. Using the FAB model, the minimum reductions in nitrogen and S deposition necessary to protect 95% of the study lakes are 32.7 and 42.1 $mmol_c \cdot m^{-2} \cdot year^{-1}$, respectively. Additional reductions beyond those proposed for 2030 are required to minimize critical load exceedance and promote recovery in alkalinity and pH of surface waters at the study catchments.

Résumé : Nous étudions la réaction chimique de 20 lacs de sommet de bassin versant en Nouvelle-Écosse à une diminution des précipitations acides à l'aide d'analyses des tendances; nous évaluons aussi la nécessité de réductions additionnelles à l'aide de deux modèles de charge critique à l'état d'équilibre. On observe depuis 1984 des réductions significatives des concentrations de sulfates (SO_4^{2-}) d'origine non marine et d'hydrogène (H^+) à quatre stations de surveillance des précipitations humides réparties dans le Canada atlantique. Les tendances dominantes dans les eaux de surface montrent une diminution des concentrations de SO_4^{2-} avec peu d'amélioration de l'alcalinité ou de l'H^+. D'après les modèles SSWC (chimie des eaux à l'état d'équilibre) et FAB (bilan d'acidité du premier ordre) et avec une limite chimique critique de capacité à neutraliser les acides de 20 $\mu mol_c \cdot L^{-1}$, la charge critique est dépassée respectivement à 9 et 13 des 20 lacs étudiés. L'application du modèle SSWC indique que les précipitations de soufre (S) doivent être réduites de 37,3 $mmol_c \cdot m^{-2} \cdot an^{-1}$ à partir des niveaux de 1997 afin d'empêcher le dépassement des charges critiques dans 95 % des lacs étudiés. Selon le modèle FAB, les réductions minimales de précipitations d'azote et de S nécessaires pour protéger 95 % des lacs étudiés sont respectivement de 32,7 $mmol_c \cdot m^{-2} \cdot an^{-1}$ et de 42,1 $mmol_c \cdot m^{-2} \cdot an^{-1}$. Des réductions plus importantes que celles proposées pour 2030 sont donc nécessaires afin de minimiser les dépassements de charge critique et de favoriser la récupération de l'alcalinité et du pH des eaux de surface dans les bassins versants étudiés.

[Traduit par la Rédaction]

Introduction

The harmful effects of acid rain came to prominence in Canada during the 1970s (Jeffries et al. 2003*a*) when surface waters in Ontario (Beamish and Harvey 1972) and the Maritimes (Gorham 1957) were losing fish populations because of acidification. Sulphate (SO_4^{2-}) deposition is the main driver of surface water acidification in eastern Canada (Jeffries et al. 2003*a*), although there has been growing concern on nitrogen (nitrate and ammonia) deposition in recent years. As a result, sulphur dioxide (SO_2) emission reduction measures have been implemented or planned in North America (e.g., the Acid Rain Control Program (1985) and the Canada–US Air Quality Agreement (1991)). The above policy instruments have been successful; SO_4^{2-} deposition in eastern Canada has decreased by approximately 40% during the past two decades, whereas nitrogen (N) deposition has remained unchanged (Jeffries et al. 2003*b*). In terrestrial ecosystems,

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N is generally a limiting nutrient and is retained; thus, current policies have not addressed the need for N reductions in Canada except in the context of localized smog reduction. In Canada, much effort has gone into monitoring the condition of affected ecosystems, with a particular focus on surface water chemistry.

Atlantic Canada is especially sensitive to acid deposition, as much of the area is underlain by bedrock types such as granites and slates that weather poorly and soils that have low acid-buffering capacities (Clair et al. 2002). To better understand acidification effects, Environment Canada has monitored the water chemistry of lakes identified as being sensitive to long-range transboundary air pollution in the region since 1983. The principal result of this initiative has been the characterization of the response of lakes to decreasing sulphur (S) emissions. Trend analysis studies have shown the importance of time window selection in detecting trends (Clair et al. 1995, 2002; Ehrman and Clair 1995). The most recent analysis (up to 1997) for the Nova Scotian lakes monitored by Environment Canada showed significant SO_4^{2-} decreases in the majority of the 72 lakes studied but concluded that recovery of alkalinity and pH was generally absent (Clair et al. 2002).

The critical load approach has been extensively used as scientific underpinning in support of emission reduction policies (Henriksen and Posch 2001). A critical load (CL) has been defined as the "highest load of acid deposition below which no damage to the specified sensitive component of biological systems will occur over the long-term" (Nilsson and Grennfelt 1988). In the 1980s, the Canadian Council of Resource and Environment Ministers had set the CL of wet SO_4^{2-} for fresh waters at 20 $kg \cdot ha^{-1} \cdot year^{-1}$ (41.6 $mmol_c \cdot m^{-2} \cdot year^{-1}$; Jeffries and Lam 1993). More recently, using a better understanding of ecological effects, a CL of <6 kg wet $SO_4^{2-} \cdot ha^{-1} \cdot year^{-1}$ was suggested as more appropriate for lakes in the Kejimkujik region of Nova Scotia (Environment Canada 1997). Recent CL estimates for south-central Ontario indicate that current levels of acid deposition are unlikely to promote widespread recovery of aquatic ecosystems (Henriksen et al. 2002; Aherne et al. 2004). These studies have been helpful in evaluating the success of emission reduction measures and identifying the need for further cutbacks.

Two steady-state models are widely used to calculate CLs for surface waters: the Steady State Water Chemistry (SSWC) model (Henriksen et al. 1992) and the First-order Acidity Balance (FAB) model (Posch et al. 1997). The SSWC model requires mean annual water chemistry and annual runoff to calculate CLs of S, whereas the FAB model simultaneously calculates CLs of S and N through the incorporation of terrestrial catchment soil processes such as uptake, immobilization, and denitrification of N while also taking into account in-lake retention of S and N.

The objectives of the study were to (*i*) evaluate recovery (increases in alkalinity and pH and decreases in SO_4^{2-}) of 20 acid-sensitive lakes in response to emissions reductions and (*ii*) quantify whether there is a need for further reductions in S and N deposition in Nova Scotia beyond those planned to prevent CLs from being exceeded. Temporal trend analysis and CLs for 20 lakes in acid-sensitive headwater catchments in Nova Scotia are presented. This updates previous trend analyses by including an additional 5 years of data.

Materials and methods

Study area

Nova Scotia, located on Canada's Atlantic coast, has a humid continental climate, while the marine waters that surround the province moderate against extreme temperatures in summer and winter. Average annual rainfall in the province is approximately 1.40 m, and 1994–1998 averages ranged from 1.36 to 1.51 m at the study lakes. Long-term mean annual air temperatures are approximately 6.5 °C across the province. In addition to influencing air temperature, the marine influence dominates the chemistry of deposition and surface waters, with ions originating from marine aerosols (Ca^{2+}, Mg^{2+}, Na^+, K^+, SO_4^{2-}, Cl^-) being elevated in deposition. Precambrian geology is typical across the province, and poorly developed podzolic soils formed from sandy parent materials are found in the region. Soil deposits are generally shallow, often overlying bedrock of Ordovician slates and Devonian–Carboniferous granites.

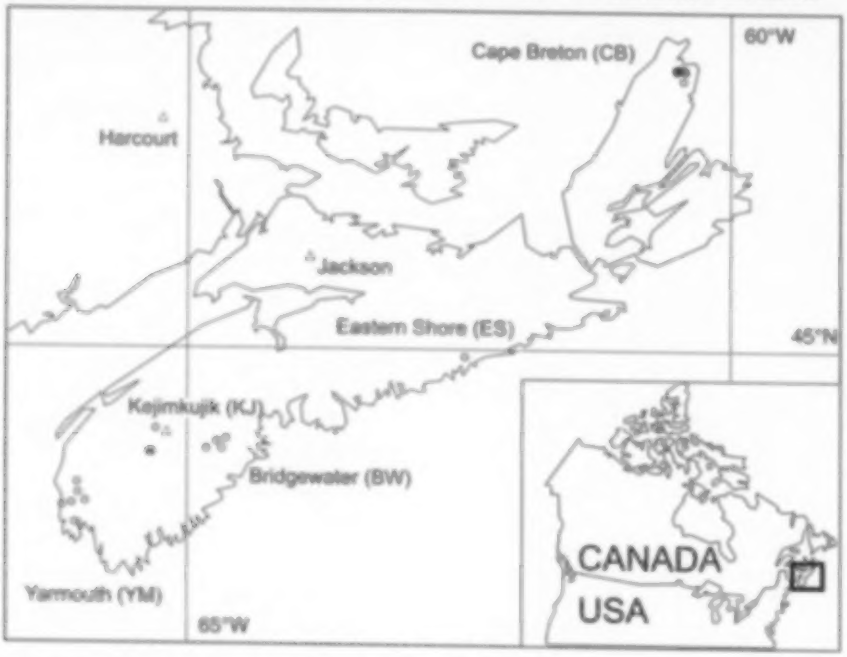
The 20 study lakes are a subset of the 72 acid-sensitive lakes monitored in Environment Canada's Atlantic region temporal monitoring network. This program selected groups of acid-sensitive lakes in areas unaffected by development (Clair et al. 2001). The lake catchments are primarily forested and grouped in five distinct regions: Yarmouth, Kejimkujik, Bridgewater, Eastern Shore, and Cape Breton (Fig. 1). In this study, all of the catchments are small, headwater catchments selected to maintain consistency in hydrologic order and size. The maximum catchment area was set at 6 km^2, and lakes were chosen to represent a wide range of water chemistry using alkalinity, dissolved organic carbon (DOC), and pH as selection criteria (Table 1). Atmospheric deposition is monitored at four Canadian Atmospheric Pollution-Monitoring Network (CAPMoN) stations in Atlantic Canada (Harcourt, New Brunswick; Baie d'Espoir, Newfoundland and Labrador; and Jackson and Kejimkujik, Nova Scotia) (Fig. 1).

Sample collection and analysis

Two samples were collected (during spring and fall turnover) from the middle of the lake in most years, with a minimum of one spring or fall sample. A single sample collected shortly after turnover has been found to be representative of average chemistry when compared with yearly flow-weighted averages (Henriksen et al. 1992). For eight lakes, data were available for 20 years (1983–2002). For the remaining 12 lakes, data were available from 1990 to 2002 (Table 1), with the exception of Allens (1983–1989 and 2004) (Table 1). Every tenth sample was collected in triplicate to ensure that laboratory techniques were within quality assurance criteria for replicates. The samples were analyzed at Environment Canada's analytical laboratory in Moncton, New Brunswick. Analytes included specific conductance, total organic carbon (TOC)/DOC, total Al, Mn^{2+} and $Fe^{2+/3+}$, Gran alkalinity, pH, NO_2^-/NO_3^-, total N, SO_4^{2-}, Ca^{2+}, Mg^{2+}, Cl^-, Na^+, and K^+. Additional details for lake sampling and laboratory analysis are given by Clair et al. (2001).

Wet deposition data was collected at the four CAPMoN stations during the period 1984–2002. Precipitation chemistry, including pH, NO_3^-, SO_4^{2-}, NH_4^+, Cl^-, Ca^{2+}, Mg^{2+}, Na^+, and K^+, was monitored through 24-hour integrated samples

Fig. 1. Location of study lakes (open circles) in the five regions and Canadian Air and Precipitation Monitoring Network deposition stations (open triangles) in Atlantic Canada. Note that Baie d'Espoir, Newfoundland and Labrador, is not shown.



collected with a wet-only precipitation collector. Charge balance acid-neutralizing capacity (ANC) of deposition was calculated as the sum of base cations minus the sum of acid anions:

$$\text{ANC} = (\text{Ca}^{2+} + \text{Mg}^{2+} + \text{Na}^{+} + \text{K}^{+}) - (\text{SO}_4^{2-} + \text{NO}_3^{-} + \text{Cl}^{-}) \quad (1)$$

Daily precipitation was measured using a type B rain gauge and a Nipher-shielded snow gauge in millimetres of water.

Data analysis was carried out on lake chemistry, and volume-weighted wet deposition averages after evaluating data quality by charge balance with ±10% set as a criterion for acceptance. It was assumed that Cl^- behaves conservatively and is of marine origin; therefore, nonmarine sources of Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, and SO_4^{2-} were estimated using standard ion:Cl^- ratios for sea salts (Werner and Spranger 1996). Additional details for lake sampling and laboratory analysis methods are given by Clair et al. (2001).

Trend analysis

The nonparametric Mann–Kendall test (Hirsch and Slack 1984) was used for detecting the presence of monotonic trends in lake and deposition chemistry. The Mann–Kendall test is commonly used to detect monotonic trends in hydrological, meteorological (Yue et al. 2002), and chemical (e.g., Evans and Monteith 2001; Wright et al. 2001) time series data. Slopes were estimated using the method of Sen (1968) as the median of all between-year differences between data values. The Mann–Kendall test is capable of accounting for missing data and serial correlation, making it robust with respect to some of the problems that commonly confound trend detection in hydrological time series (Hirsch and Slack 1984).

Two windows were used for trend analysis, 1983–2002 and 1990–2002, corresponding to the data records available for the lakes. Allens Lake was analyzed from 1983 to 1989. To ensure consistency of approach, similar time windows were used to analyze the CAPMoN wet deposition data (limited to 18 years). Deposition chemistry variables selected for trend analysis included Cl^- nonmarine SO_4^{2-} and Ca^{2+}, H^+, NO_3^-, NH_4^+, and ANC. Lake chemistry was analyzed for trends in Cl^-, nonmarine SO_4^{2-} and Ca^{2+}, H^+, and Gran alkalinity. Chloride trends were investigated to identify potential change in sea-salt influence over the study period. The latter four variables were chosen for analysis because they serve as valuable indicators of catchment response to acid deposition. Calcium was used as a surrogate for base cation behaviour. Additionally, trends in DOC concentration were evaluated for the period 1994–2002. Owing to changes in analytical procedures, DOC data prior to 1994 were not included in the analysis. To identify both increasing and decreasing trends, two-sided significance tests were used. An alpha value of 0.05 was used as the minimum level of significance for all tests. In addition, nonsignificant trends were also discussed in instances where all or almost all of the study lakes showed slopes in the same direction; multiple small (nonsignificant) changes in concentrations of several ions may account for significant changes in concentration of other ion(s).

CLs

The SSWC and FAB models were used to calculate CLs for the study lakes. The SSWC model is largely empirical, while the FAB model is partially process-oriented. The SSWC model (Henriksen et al. 1992) estimates the CL of S based

Table 1. Five-year (1998–2002) mean annual lake concentrations for calcium, magnesium, sodium, potassium, sulphate, chloride, Gran alkalinity (Alk) (all units of $\mu mol_c \cdot L^{-1}$); dissolved organic carbon (DOC, $mg \cdot L^{-1}$); mean pH and precipitation volume (PPT, m); long-term runoff (*Q*, m); and lake retention time (RT, years) for the 20 study lakes.

Region–lake	Data years	Ca^{2+}	Mg^{2+}	Na^+	K^+	SO_4^{2-}	Cl^-	Alk	DOC	pH	PPT	*Q*	RT
Yarmouth													
Allens[a]	8	48	109	531	22	44	611	99.1	5.2	5.93	1.36	0.96	0.01
Bird	20	28	34	211	11	36	231	84.5	2.7	6.62	1.38	0.98	0.51
Brenton	20	77	78	323	13	83	340	20.2	17.5	4.97	1.38	0.98	0.14
Jesse	20	67	86	236	15	64	277	41.6	4.8	6.19	1.38	0.98	0.35
Tedford	20	75	79	329	12	74	365	50.0	2.8	6.32	1.36	0.97	0.43
Trefry	20	94	104	302	14	84	325	86.7	5.9	6.42	1.38	0.99	0.94
Kejimkujik													
Beaverskin	20	18	30	113	6	43	107	−6.9	2.4	5.44	1.39	1.00	0.87
Big Dam East	20	35	37	132	5	43	121	13.1	4.2	6.02	1.39	1.00	0.01
Pebbleloggitch	20	16	27	113	5	41	105	−31.8	10.8	4.50	1.39	1.00	0.30
Bridgewater													
Annis	13	81	55	117	6	53	125	66.6	1.6	6.65	1.43	1.05	2.50
Huey	13	42	35	126	2	50	120	10.9	3.6	5.76	1.43	1.05	0.03
Little Wiles	13	51	52	120	6	100	119	22.3	2.1	5.24	1.44	1.05	0.10
Matthew	13	60	61	245	11	67	249	−2.5	7.0	5.70	1.43	1.05	0.22
Eastern Shore													
Halfway	13	46	34	127	5	48	126	8.2	5.0	5.46	1.51	1.13	0.50
Cape Breton													
Branch	13	28	34	154	8	36	156	−40.5	9.8	4.75	1.44	1.06	0.06
Glasgow	13	24	32	145	8	31	149	−3.3	7.0	4.93	1.44	1.06	2.31
John Dee	13	44	43	157	7	32	148	29.6	9.2	5.35	1.44	1.06	0.34
Long Pond	13	81	57	174	13	46	171	88.9	3.3	6.00	1.44	1.06	0.01
Mica Hill	13	59	36	159	8	37	146	61.3	9.8	5.27	1.44	1.06	0.04
Round	13	29	34	144	7	32	133	0.9	8.1	5.13	1.44	1.06	0.04
Mean	13	50	53	198	9	52	206	29.9	6.1	5.63	1.42	1.03	0.48

Note: Measurements of NO_3^- and NH_4^+ were at or below detection limits for all study lakes.

[a] Lake chemistry is for 2004.

on the current base cation flux from the catchment. The FAB model (Posch et al. 1997) uses a simple mass balance that takes into account N dynamics in the terrestrial catchment to calculate CLs of S and N for fresh waters. Both models use nonmarine ion concentrations and specify a critical chemical criterion to protect the biological indicator from long-term damage as the minimum acceptable level necessary to protect aquatic biota.

The current application follows the most recent published descriptions for both models (Henriksen and Posch 2001). Five-year mean annual lake chemistry (1998–2002; 2004 for Allens Lake) and long-term average runoff volume (Environment Canada 1978) were used to calculate the SSWC critical load of acidity (CL(A)):

$$CL(A) = (BC_0 - ANC_{limit})Q \tag{2}$$

where Q is the long-term mean annual runoff, and ANC_{limit} is the critical chemical limit for acid-neutralizing capacity. BC_0 is the background weathering concentration estimated from the present base cation concentration minus the long-term changes in base cation concentration, inferred from the inputs of strong acid anions. For further details, see Henriksen and Posch (2001), Henriksen et al. (2002), and Watmough and Dillon (2002).

In Canada, 40 $\mu mol_c \cdot L^{-1}$ has been applied as an acceptable ANC (Henriksen et al. 2002). However, an ANC_{limit} of 20 $\mu mol_c \cdot L^{-1}$ derived from an empirical relationship between lake water chemistry and fish status in Norway (Lien et al. 1992) is widely applied (e.g., Russia: Moiseenko 1994; Southern Alps: Boggero et al. 1998; China: Duan et al. 2000; Ireland: Aherne and Curtis 2003). Given that previous modelling studies predicted many lakes to have low historic ANC (Clair et al. 2003) and that the protection of fish stocks is a priority in Nova Scotia, an ANC of 20 $\mu mol_c \cdot L^{-1}$ was chosen as the critical chemical criterion in the SSWC (and FAB) model.

The FAB model takes N processes into account, and therefore it does not provide a unique CL value, as varying levels of S and N deposition can be combined to meet the CL. Accordingly, the CL is defined by a critical load function (CLF), which consists of all possible pairs of S and N deposition for which the CL is met. Endpoints of the function are governed by the maximum deposition of S or N while the corresponding N and S depositions are held at zero (i.e., the endpoints are the CLs of deposition for S or N alone). The area under the curve represents all possible combinations of S and N deposition for which there is no exceedance. The CLF is defined as

$$(1 - p_S)S_{dep} + (1 - p_N)b_N N_{dep} = (1 - p_N)M_N + CL(A) \tag{3}$$

Table 2. Trends (p values shown in parentheses) in precipitation volume (mm·year^{-1}) and hydrogen, nonmarine sulphate, nonmarine calcium, chloride, acid-neutralizing capacity (ANC), nitrate, and ammonium concentrations (µmol$_c$·L^{-1}·year^{-1}) at four precipitation monitoring stations in Atlantic Canada.

	Kejimkujik	Jackson	Harcourt	Baie d'Espoir
1990–2002				
Precipitation	−0.61 (0.67)	1.30 (0.50)	0.16 (1.00)	−1.91 (0.43)
H^+	−0.41 (0.12)	−0.33 (0.10)	**−0.65 (0.01)**	**−0.41 (0.01)**
SO_4^{2-}	−0.14 (0.30)	−0.10 (0.62)	−0.30 (0.11)	−0.26 (0.08)
Ca^{2+}	−0.21 (0.95)	0.24 (0.43)	0.11 (0.58)	−0.19 (0.90)
Cl^-	0.02 (0.43)	0.04 (0.06)	**0.05 (<0.01)**	0.01 (0.16)
ANC	0.23 (0.43)	0.08 (0.86)	0.37 (0.11)	0.32 (0.16)
NO_3^-	0.04 (0.58)	0.06 (0.50)	0.02 (0.84)	−0.01 (0.58)
NH_4^+	0.11 (0.13)	0.06 (0.20)	0.07 (0.30)	0.03 (0.50)
1984–2002				
Precipitation	0.31 (0.67)	1.51 (0.16)	0.86 (0.40)	0.58 (0.76)
H^+	**−0.71 (0.01)**	**−0.33 (0.01)**	**−0.83 (<0.01)**	**−0.40 (0.03)**
SO_4^{2-}	**−0.57 (<0.01)**	**−0.37 (0.01)**	**−0.56 (<0.01)**	**−0.38 (<0.01)**
Ca^{2+}	−0.19 (0.73)	0.20 (0.20)	−0.07 (0.68)	0.00 (0.52)
Cl^-	−0.03 (0.12)	−0.00 (1.00)	−0.01 (0.60)	−0.21 (1.00)
ANC	0.37 (0.12)	0.14 (0.62)	0.61 (0.08)	0.32 (0.08)
NO_3^-	−0.05 (0.58)	0.02 (0.70)	−0.04 (0.76)	0.00 (0.94)
NH_4^+	−0.01 (0.78)	0.01 (0.89)	−0.02 (0.82)	−0.03 (0.45)

Note: Trends shown in bold are significant at $\alpha \le 0.05$. Adjustments to p values to account for multiple testing were not performed so that the presentation of these results is comparable with previous analyses (i.e., Clair et al. 1995, 2002).

where ρ_S and ρ_N are dimensionless in-lake retention factors for S and N, modelled by a kinetic equation based on runoff, lake:catchment ratio, and the net mass transfer coefficients for S and N (Kelly et al. 1987). Values for mass transfer coefficients used to represent in-lake retention of S (0.5 m·year^{-1}) and N (5 m·year^{-1}) were reported by Baker and Brezonik (1988) and Dillon and Molot (1990), respectively. The coefficients b_N and M_N depend on the denitrification fraction in soils, net N uptake, and net N immobilization and are a function of the magnitude of N deposition (N_{dep}). Long-term immobilization of N was set to 3.57 mmol$_c$·m^{-2}·year^{-1} (Umweltbundesamt 2004), and N uptake was set to zero under the assumption that there is no net increase in biomass. A linear equation was used to calculate denitrification from the wetland area in each catchment. The area of wetland was estimated using a relationship between lake DOC concentration and catchment peat cover as described by Dillon and Molot (1997). Forest and grassland areas were estimated from site observations. Finally, CL(A) is the critical load of acidity estimated using the SSWC model. For additional details, see Henriksen and Posch (2001).

CL exceedance, or the amount of deposition a catchment receives over and above its CL, can be calculated by comparing CL and acid deposition (SSWC: SO_4^{2-}; FAB: SO_4^{2-} + NO_3^- + NH_4^+). The SSWC model can also take N into account by incorporating N leaching into the exceedance estimate; however, as all N is currently retained at the study catchments, this term does not influence the exceedance calculations. For the FAB model, exceedance is calculated as exceedance leaching, which is the leaching of acidity above the critical chemical limit of ANC. Exceedance of the CL has no unique solution, but rather many combinations of reductions in S and N may meet the CL. For simplicity, the minimum reductions in each of S and N (the shortest distance between deposition and the CLF) are reported here. A deposition grid map available from Environment Canada (Ro and Vet 2003) was used to estimate current (1994–1998) deposition at the catchments. Inputs for SO_4^{2-} and N in wet deposition (at a resolution of approximately 45 km × 45 km) and dry deposition (at a resolution of approximately 35 km × 35 km) were interpolated to a common grid resolution (25 km × 25 km) and combined to produce total deposition estimates for nonmarine SO_4^{2-} and N. Exceedance was also calculated for 2030 using a recently proposed future emission scenario (WxPrime Corporation 2004). Sulphate deposition forecasts were derived from the proposed emission reduction estimates using the Acid Deposition and Oxidant Model (ADOM: Kaminski 2002; Environment Canada 2004). The proposed reductions roughly correspond to a 50% reduction in SO_4^{2-} deposition by 2030 from 2000 baselines and no change in N emissions. Further details are given in the 2004 Canadian Acid Deposition Science Assessment (Environment Canada 2004).

Results and discussion

Atmospheric deposition trends

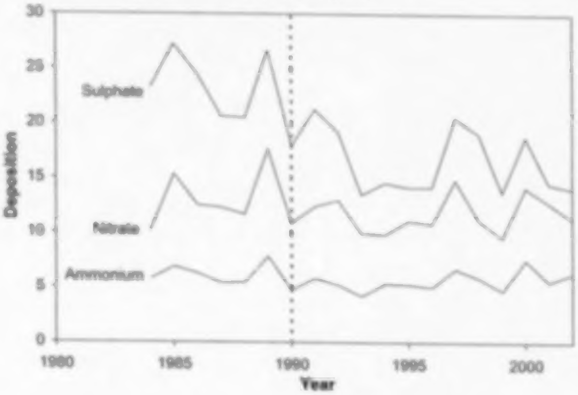
There was a significant decrease in SO_4^{2-} concentration from 1984 to 2002 (Table 2) at all four CAPMoN stations. This is consistent with Clair et al. (2002), who carried out trend analyses for the period 1984–1997. Driscoll et al. (2003) reported long-term decreases in SO_4^{2-} and H^+ in deposition in the Adirondacks for the period 1979–2000. Neither Clair et al. (2002) nor this study found decreases in

SO_4^{2-} during the most recent periods (beginning in 1989 or 1990). Canada met its air quality agreement targets by 1993, and in 1997 US emissions were below target levels (Jeffries et al. 2003*a*). Further emission reductions are scheduled to take place post-2000. Lack of a significant trend over the past decade indicates that smaller reductions in S emissions have had a minimal impact on deposition chemistry (Fig. 2).

Consistent with decreases in SO_4^{2-}, all sites showed decreases in H^+ during the period 1984–2002, while two stations showed decreases in H^+ from 1990–2002, a clear indication that the pollution abatement programs were successful in reducing acid deposition. It is important to note that the decreases in H^+ observed were equal to or greater than the decreases in SO_4^{2-}. This suggests that decreases in base cation concentration, which often accompany decreases in SO_4^{2-}, are not offsetting decreases in the acidity of precipitation. Previous trend analyses did not detect a H^+ trend for the period 1984–1997 (Clair et al. 2002). The addition of 5 years to the data series may have improved power of trend detection, allowing for detection of H^+ trends during the period 1984–2002.

Precipitation Cl^- concentrations demonstrate different slopes over the two time periods. Chloride concentrations have an increasing slope over the short term, with the increase at Harcourt being significant and the long term showing decreasing slopes at all four sites. Increasing slopes were observed for ANC concentrations across all four sites during the two time windows, again an indication that strong acid (SO_4^{2-}) concentrations are decreasing faster than the concentrations of base cations.

Fig. 2. Wet deposition of sulphate (SO_4^{2-}), nitrate (NO_3^-), and ammonium (NH_4^+) ($\mu mol_c \cdot L^{-1}$) at Kejimkujik Canadian Air and Precipitation Monitoring Network station, Nova Scotia, for the period 1984–2002. Broken line at 1990 indicates division between two time periods for trend analysis.



Lake chemistry trends

It was important to select lakes representing a wide range in alkalinity, DOC, and pH to account for different lake responses to acid deposition (Table 1). Lakes with high alkalinities may exhibit little change in pH and alkalinity in response to acid deposition compared with lakes with low alkalinity and little ability to neutralize incoming acid anions. Lake DOC concentration may also influence response, as lakes with high DOC levels should be more resistant to changes in pH through anthropogenic acidification and likewise may also take longer to respond to reductions in acid deposition (Howell 1989).

Geology, wetland coverage, distance from the ocean, and deposition are the major factors responsible for the wide range in alkalinity, DOC, and pH observed in the lakes. The mean Gran alkalinity (30 $\mu mol_c \cdot L^{-1}$) is indicative of the extremely low ability of the lakes to neutralize incoming acid. Some lakes, such as Branch in Cape Breton, have very low alkalinity (–41 $\mu mol_c \cdot L^{-1}$), corresponding to very limited carbonate buffering capacity. It is possible that some of the study lakes were once strongly affected by acidic deposition (i.e., were intolerant to incoming acid) and what little buffering capacity they had was consumed and at present are little affected by continuing acidic deposition. The high concentrations of Na^+ and Cl^- are evidence of the sea-salt influence on lake chemistry (Table 1).

Lakes with the full 20-year data set are considered to give the best indication of surface water response to changes in atmospheric deposition, particularly as the largest decreases in emissions occurred prior to 1990. Decreases in lake SO_4^{2-} concentrations were common at the study lakes, and trends in SO_4^{2-} were observed for seven of nine lakes where monitoring began in 1983 (Table 3). Over the period 1990–2002, fewer trends in SO_4^{2-} were observed (five lakes; Table 3); however, the slopes indicate a general decrease in SO_4^{2-} concentration (13 lakes). These patterns are consistent with deposition and indicate that a greater decrease in S occurred in the 1980s with minimal changes thereafter. While the slopes indicate a decrease in SO_4^{2-} deposition for the 1990–2002 period, the decrease in SO_4^{2-} concentrations in the lakes was likely also influenced by earlier decreases in deposition. Some of this delay may be attributed to the lake retention times (Table 1); however, as these times are generally short, variable retention of SO_4^{2-} in the catchments may play a larger role. Dillon and Lazerte (1992) reported that SO_4^{2-} does not act conservatively and is influenced by climatic variability. Clair et al. (2002) reported similar SO_4^{2-} decreases in approximately 50% of the lakes studied.

Despite decreasing trends in H^+ deposition, few lakes show a corresponding statistically significant decrease in H^+: one for the full 20-year period and two for the shorter period (Table 3). However, nonsignificant, decreasing H^+ slopes are observed at many lakes. The minimal improvement in lake pH is cause for concern, as lake pH is an important factor affecting acid-sensitive biota, and improvement in pH and alkalinity are often the targets for stakeholders. The limited improvement in pH, despite declining SO_4^{2-} concentrations, is consistent with the observations of Clair et al. (2002). The dystrophic nature of many catchments may explain some of the divergence, as lakes with high DOC levels are more resistant to changes in pH because of the buffering ability of DOC and may take longer to respond to reductions in acid deposition (Howell 1989). Driscoll et al. (2003) found that increases in DOC were responsible for increased natural acidity, which counteracted some of the decrease in anthropogenic acidity. In the current study, analysis of the limited DOC data for the study lakes (1994–2002) did not reveal any increasing trends.

Trends in alkalinity were rare although decreasing slopes were common across both time periods (Table 3). While

Table 3. Trends (*p* values shown in parentheses) in nonmarine calcium, chloride, Gran alkalinity (Alk), nonmarine sulphate, and hydrogen concentrations ($\mu mol_c \cdot L^{-1} \cdot year^{-1}$) at the 20 study lakes.

Region–lake	Ca^{2+}	Cl^-	Alk	SO_4^{2-}	H^+
1990–2002					
Yarmouth					
Bird	0.92 (0.16)	0.79 (0.95)	–0.10 (0.85)	**–1.06 (0.01)**	–0.01 (0.07)
Brenton	0.39 (0.85)	7.56 (0.16)	–0.34 (0.81)	–0.97 (0.30)	–0.23 (0.85)
Jesse	0.55 (0.36)	3.99 (0.36)	0.00 (1.00)	**–1.81 (0.01)**	–0.03 (0.08)
Tedford	0.32 (0.76)	7.23 (0.43)	–0.36 (0.27)	–0.93 (0.13)	–0.01 (0.30)
Trefry	–0.86 (0.20)	1.34 (0.62)	–0.24 (0.85)	**–1.91 (<0.01)**	–0.00 (0.95)
Kejimkujik					
Beaverskin	–0.05 (0.76)	0.90 (0.43)	–1.21 (0.13)	–0.45 (0.08)	–0.05 (0.33)
Big Dam East	0.45 (0.25)	0.52 (0.67)	–0.71 (0.14)	–0.43 (0.25)	–0.03 (0.14)
Pebbleloggitch	–0.10 (0.20)	0.94 (0.36)	**–1.21 (0.03)**	–0.68 (0.13)	0.20 (0.50)
Bridgewater					
Annis	**1.15 (0.02)**	0.18 (0.81)	**1.18 (0.01)**	–0.41 (0.43)	–0.01 (0.08)
Huey	0.24 (0.50)	1.69 (0.13)	–0.79 (0.09)	**–1.74 (<0.01)**	0.00 (1.00)
Little Wiles	–1.19 (0.10)	0.36 (0.81)	–0.14 (0.95)	–2.79 (0.06)	**–0.46 (0.04)**
Matthew	0.74 (0.10)	**5.83 (0.04)**	–0.06 (0.71)	**–1.79 (0.02)**	**–0.08 (0.05)**
Eastern Shore					
Halfway	0.39 (0.13)	1.48 (0.30)	**–0.80 (0.04)**	–0.32 (0.20)	–0.03 (0.62)
Cape Breton					
Branch	0.18 (0.76)	2.79 (0.36)	–0.06 (1.00)	–0.26 (0.58)	–0.01 (0.90)
Glasgow	**0.29 (0.03)**	–0.09 (0.95)	–0.34 (0.71)	–0.50 (0.13)	0.05 (0.81)
John Dee	0.71 (0.20)	1.09 (0.46)	0.46 (0.67)	–0.59 (0.13)	–0.07 (0.71)
Long Pond	0.62 (0.50)	2.48 (0.67)	1.39 (0.25)	–0.55 (0.30)	–0.00 (0.58)
Mica Hill	1.33 (0.15)	2.00 (0.46)	0.61 (0.39)	0.02 (1.00)	–0.69 (0.13)
Round	0.04 (1.00)	0.43 (0.76)	–0.30 (0.67)	–0.58 (0.20)	–0.38 (0.30)
1983–2002					
Yarmouth					
Allens[a]	**2.95 (0.05)**	6.49 (0.33)	**5.66 (0.03)**	**–4.87 (<0.01)**	–0.03 (0.15)
Bird	–0.26 (0.36)	–0.45 (0.90)	–0.50 (0.12)	**–1.01 (0.01)**	–0.01 (0.08)
Brenton	–0.43 (0.38)	2.95 (0.11)	–0.01 (0.92)	**–4.25 (<0.01)**	–0.06 (0.75)
Jesse	–0.34 (0.21)	0.33 (0.79)	–0.07 (0.70)	**–1.18 (<0.01)**	**–0.02 (0.03)**
Tedford	–0.60 (0.10)	7.14 (0.03)	**–0.59 (0.01)**	–0.77 (0.11)	–0.01 (0.30)
Trefry	–0.38 (0.28)	–1.99 (0.27)	0.00 (1.00)	**–0.98 (<0.01)**	–0.01 (0.13)
Kejimkujik					
Beaverskin	–0.07 (0.23)	–0.72 (0.23)	–0.50 (0.12)	–0.03 (0.80)	0.04 (0.38)
Big Dam East	–0.27 (0.26)	–0.75 (0.26)	–0.12 (0.62)	**–0.48 (0.01)**	–0.02 (0.06)
Pebbleloggitch	–0.06 (0.11)	–0.26 (0.11)	0.00 (0.95)	**–0.39 (0.05)**	0.00 (0.79)

Note: Trends shown in bold are significant at $\alpha \le 0.05$. Adjustments to *p* values to account for multiple testing were not performed, so that the presentation of these results is comparable with previous analyses (i.e., Clair et al. 1995, 2002).

[a] Trends reported are for 1983–1989.

lakes with decreasing SO_4^{2-} may show increases in alkalinity. Dillon and Evans (2001), Stoddard et al. (1999), and Jeffries et al. (2003*a*) reported that alkalinity in eastern Canada is showing little response to changes in atmospheric deposition. This has been attributed to decreasing base cation deposition and decreasing leaching because of soil acidification that coincide with decreasing SO_4^{2-} deposition (Stoddard et al. 1999). Evidence exists that base cation trends in lakes sometimes match SO_4^{2-} trends (Clair et al. 2002). Over the full 20-year data period, all lakes show decreasing slopes in Ca^{2+} concentrations (Table 3). This appears to be an important factor offsetting the decreases in SO_4^{2-}, thereby limiting increases in alkalinity in the study lakes. Over the 1990–2002 period, however, positive slopes in Ca^{2+} concentrations were common and inconsistent with observed trends in SO_4^{2-} and alkalinity (Table 3). Other studies in North America over the same period found decreases in base cation concentrations (Driscoll et al. 2003; Watmough and Dillon 2003; Watmough et al. 2005). During this period, the decreases in alkalinity and increases in Ca^{2+} appear to be driven by deposition of sea salts, as Cl^- slopes increased at all but one catchment. This is consistent with Cl^- deposition patterns, which also showed increasing slopes over this period. During a sea-salt episode, when deposition of sea-salt is elevated, influx of marine Na^+ can displace Ca^{2+} from soil exchange sites and into soil and surface waters, resulting in elevated lake Ca^{2+} concentrations. This study only considered wet deposition, and in coastal areas, dry deposition of sea salt to forest ecosystems in Nova Scotia is considerable (Yanni et al. 2000). This may account for the Ca^{2+} trends

Table 4. Five-year (1998–2002) mean annual sulphate (SO_4^{2-}) and nitrogen ($NO_3^- + NH_4^+$) deposition and critical loads (CL(A)), and exceedances (Ex) (all data in units of $mmol_c \cdot m^{-2} \cdot year^{-1}$) calculated using the Steady State Water Chemistry (SSWC) and the First-order Acidity Balance (FAB) models, where positive values denote critical load exceedance.

	Deposition		SSWC			FAB		
Region–lake	SO_4^{2-}	$NO_3^- + NH_4^+$	CL(A)	Ex 1997	Ex 2030	CL(A)	Ex_{le} 1997	Ex_{le} 2030
Yarmouth								
Allens	39.5	36.8	7	32	16	8	43	26
Bird	39.5	36.8	83	–44	–60	93	–41	–58
Brenton	39.5	36.8	45	–6	–22	48	11	–6
Jesse	39.5	36.8	62	–23	–39	67	–10	–27
Tedford	38.0	32.6	43	–5	–21	50	–4	–19
Trefry	39.4	34.9	91	–52	–69	105	–56	–72
Kejimkujik								
Beaverskin	38.2	37.9	1	37	21	1	44	30
Big Dam East	37.5	37.3	20	18	2	22	28	13
Pebbleloggitch	38.2	37.9	0	42	26	0	57	41
Bridgewater								
Annis	35.2	35.7	87	–51	–66	103	–60	–73
Huey	35.2	35.7	26	9	–6	27	34	18
Little Wiles	35.1	35.4	37	–1	–16	38	16	1
Matthew	35.2	35.7	41	–6	–21	42	16	0
Eastern Shore								
Halfway	32.4	31.2	32	0	–14	35	11	–3
Cape Breton								
Branch	27.1	23.6	5	22	10	5	40	27
Glasgow	27.1	23.6	0	27	15	0	38	26
John Dee	27.1	23.6	37	–10	–21	39	–1	–13
Long Pond	27.1	23.6	74	–47	–59	75	–28	–41
Mica Hill	27.1	23.6	41	–14	–26	42	4	–9
Round	27.1	23.6	13	14	3	13	31	18
Mean	34.2	32.1	37	–3	–17	41	9	–6

Note: For the FAB model, Ex_{le} is defined as the leaching of acidity above the critical chemical limit of acid-neutralizing capacity.

observed, and in particular for Allens Lake between 1983 and 1989 (Table 3), as it is within several hundred metres of the ocean. Inputs of Cl^- from dry deposition likely account for the increase in lake Cl^- during the 1990s. Evans et al. (2001) also reported increasing Cl^- deposition during the late 1990s. The general lack of increases in alkalinity are consistent with observations made by Clair et al. (2002), who reported little change in alkalinity, with a number of lakes showing decreasing trends. This is a strong indication that acid-sensitive surface waters in Nova Scotia are not recovering in response to decreasing S deposition.

Wet precipitation Cl^- concentrations exhibited increasing slopes during 1990–2002, which appears to be the driving force behind increasing trends in lake Cl^- (Table 3). The North Atlantic Oscillation, which exhibits decadal periodicity, may be responsible for higher Cl^- concentrations during the late 1990s (Evans et al. 2001). In contrast, over the 20-year period, precipitation Cl^- concentrations showed decreasing slopes, and the majority of lake Cl^- concentrations also demonstrated decreasing slopes (Tables 2, 3).

CLs

Mean annual total (wet plus dry) nonmarine S and N deposition in Nova Scotia for the period 1998–2002 was 66.3 $mmol_c \cdot m^{-2} \cdot year^{-1}$ (approximately equally divided between N and S; Table 4). The highest N deposition was in Kejimkujik (37.9 $mmol_c \cdot m^{-2} \cdot year^{-1}$); the lowest was in Cape Breton (23.6 $mmol_c \cdot m^{-2} \cdot year^{-1}$). Sulphur deposition was highest in Yarmouth (39.5 $mmol_c \cdot m^{-2} \cdot year^{-1}$) and lowest in Cape Breton (27.1 $mmol_c \cdot m^{-2} \cdot year^{-1}$) (Table 4). This southwest to northeast gradient in anthropogenic S reflects the increasing distance from principal point sources in the eastern United States and Canada.

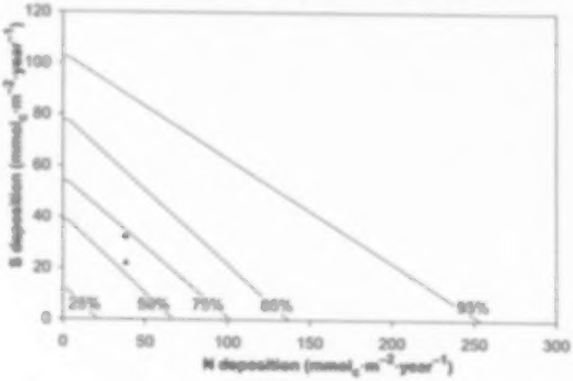
CLs calculated with the SSWC were generally below or close to current S deposition. Mean SSWC critical load was 37.1 $mmol_c \cdot m^{-2} \cdot year^{-1}$ with a range of 0–81 $mmol_c \cdot m^{-2} \cdot year^{-1}$ (Table 4). Pebbleloggitch and Glasgow had CL values of 0 $mmol_c \cdot m^{-2} \cdot year^{-1}$, which suggests that the critical chemical limit may be too high at these catchments and that they are incapable of neutralizing anthropogenic acidifying deposition above the regional background level of 10–15 $mmol_c \cdot m^{-2} \cdot year^{-1}$. CL is dependant upon both the weathering rate and the choice of acceptable critical chemical limit. If weathering rate is zero or the background ANC value is equal to or below the critical chemical limit used in the CL calculation, then the CL value will be zero (CL value cannot be negative). Incorporation of estimates of pre-acidification ANC for each catchment would improve the accuracy of the ANC_{limit} used in the CL model, thereby improving the quality of the estimates. At current (1997) levels, S deposition exceeds CLs at 9 of 20 lakes (Table 4). Furthermore, the grouping of the catchments by region reveals variable sensitivity to acid deposition. Few lakes in Yarmouth and Bridgewater have CL exceedances, while all three lakes in Kejimkujik and three of six lakes in Cape Breton receive deposition in excess of or close to their CLs.

CLs predicted with the FAB model are higher than the SSWC critical loads (mean = 40.5 mmol$_c$·m^{-2}·year^{-1}; Table 4) because the FAB model includes processes such as N immobilization and denitrification, which neutralize some of the incoming acidity (Table 4). Thirteen lakes (65%) show CL exceedance leaching in 1997 (Fig. 3), indicating that the lakes remain unable to neutralize all incoming acidity and there is limited capacity for recovery. Both models include S deposition in their calculations; however, the difference in the levels of exceedance between the two models is due to the inclusion of N deposition in FAB exceedance calculations, whereas the SSWC considers only current NO_3^- leaching. In relation to N, the SSWC model represents the best-case scenario, where N is assumed to be retained indefinitely. Currently N is retained almost quantitatively at the study lakes; however, its long-term behaviour in soils is complex (Dillon and Molot 1990; Wright et al. 2001) and is open to debate. The FAB model addresses this through the inclusion of N processes that specifies only partial retention (through immobilization and denitrification estimates that reflect differences in land cover and lake to catchment ratio) in the long term, suggesting that catchments have a limited capacity to retain N and that at some point in time, N deposited on the catchment will leach to surface waters.

To protect the majority of the study lakes, further reductions in deposition beyond that forecast for 2030 are required, based on the assumption that S deposition will be 50% of current levels and N deposition will not change (WxPrime Corporation 2004). Even with future emissions reductions, many lakes are expected to receive acidic deposition in 2030 in excess of their CL using the SSWC (7 lakes) and FAB (10 lakes) models (Table 4). Further deposition reductions are warranted to allow chemistry of acidified lakes to return to an acceptable ANC (20 µmol$_c$·L^{-1}). The SSWC model predicts that a reduction in SO_4^{2-} deposition of 37.3 mmol$_c$·m^{-2}·year^{-1} from 1997 levels is necessary to protect 95% (19) of the lakes. As these reductions would require elimination of nearly all S deposition, it is possible that the critical ANC$_{limit}$ of 20 µmol$_c$·L^{-1} is greater than the pre-acidification ANC for some of the study lakes. Protection of 75% (15) of the lakes would require a SO_4^{2-} deposition reduction of only 18.9 mmol$_c$·m^{-2}·year^{-1}. Deposition reductions calculated by the FAB model could be any combination of N and S that reduces the deposition below the CL. For simplicity, the smallest reduction (i.e., the shortest distance between the current deposition and the CLF) necessary to eliminate exceedance is reported. The FAB model indicates that reductions of 32.7 mmol$_c$·m^{-2}·year^{-1} (N) and 42.1 mmol$_c$·m^{-2}·year^{-1} (S) from 1997 levels are necessary to eliminate CL exceedance at 95% (19) of the lakes. Protection of 75% (15) of the lakes would require reductions of 17.5 mmol$_c$·m^{-2}·year^{-1} (N) and 28.1 mmol$_c$·m^{-2}·year^{-1} (S).

Currently, seven lakes have alkalinity below 20 µmol$_c$·L^{-1} (Table 1). Given that the SSWC and FAB models predict that CLs at 7 and 10 lakes, respectively, are exceeded under the proposed emission reduction scenario, it is expected that these lakes will eventually drop below the critical limit of 20 µmol$_c$·L^{-1}. The subset of 20 study lakes appears to be slightly less sensitive than the 72 acid-sensitive lakes monitored by Environment Canada in Nova Scotia (median Gran alkalinity = 22.3 µmol$_c$·L^{-1}, DOC = 5.2 mg·L^{-1}, and pH = 5.6 compared with 5.6 µmol$_c$·L^{-1}, 5.5 mg·L^{-1}, and 5.1, respectively, for the temporal monitoring network). It is important to note that these lakes were not chosen to be representative of all lakes in Nova Scotia. A wider survey of lakes in the study area is necessary to relate the observations for this set of lakes to the population of lakes in the province. If the study lakes represent only the most sensitive of lakes in the province, emission reductions may not be necessary; however, if these acid-sensitive lakes are representative of a large proportion of lakes in Nova Scotia, emissions reductions are warranted to reduce CL exceedance in the province and protect the surface waters from future degradation. Research is currently underway to investigate the sensitivity of lakes to acid deposition across the region. Jeffries and Ouimet (2004) reported that 40% of terrestrial area in the province is acid-sensitive, indicating the potential for many lakes and rivers to also be sensitive. In addition, Nova Scotia has lost the highest percentage of fish habitat to acidification than any other province (Watt 2000). These findings support our suggestion that additional emission reductions may be warranted.

Fig. 3. Percentile critical load functions predicted by the First-order Acidity Balance model, 1997 average deposition (mmol$_c$·m^{-2}·year^{-1}) for the region (solid circle), and forecasted 2030 average deposition for the region (solid triangle).



Steady-state modelling has proven to be valuable for calculating acceptable levels of acid deposition for sensitive ecosystems. Further investigation of the terrestrial CLs for these lakes would help to identify whether the lakes or soils are more sensitive to acidification. Dynamic modelling would provide additional support for emissions reductions by predicting possible time frames for recovery. Dynamic models such as MAGIC (Model of Acidification of Groundwater in Catchments; Cosby et al. 1985) are extensively used in Europe and North America for describing both initial pre-industrial conditions of lakes and assessing time to recovery under different deposition scenarios (Cosby et al. 2001; Clair et al. 2003). This would help to quantify the relative amounts of chemical recovery individual lakes have experienced to date or could potentially experience in the future.

In conclusion, during the past two decades, wet deposition SO_4^{2-} and H^+ concentrations declined across the region. Despite decreases in SO_4^{2-} at many study lakes, improvements in alkalinity and pH were largely absent, and decreasing alkalinity was observed at numerous sites possibly because of decreasing base cation inputs and sea-salt episodes. Many of the study lakes are highly sensitive to acid deposition and have low ANCs. As a result, the choice of a critical limit is crucial. CLs calculated with the SSWC and FAB models indicate that acid deposition currently exceeds CL at a large proportion of the study lakes and that additional reductions in S and (or) N emissions are necessary to reduce acid deposition to avoid exceedance at the majority of the lakes.

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Using thalweg profiling to assess and monitor juvenile salmon (*Oncorhynchus* spp.) habitat in small streams

Brent Mossop and Michael J. Bradford

Abstract: Thalweg profiles are longitudinal profiles of the streambed elevation measured along the deepest portion of the stream. This technique has recently been advocated as a tool to assess and monitor fish habitat in streams because metrics calculated from thalweg profiles can provide useful information on habitat quality, and measurements are both repeatable and independent of stream flow. Relations between thalweg metrics and land use have also been documented. However, a relation between fish abundance and thalweg metrics has not been established. To develop this relation, we surveyed thalweg profiles and sampled juvenile Chinook salmon (*Oncorhynchus tshawytscha*) density in 14 reaches of small tributary streams of the upper Yukon River. Chinook salmon density was correlated with three thalweg metrics. Two of these metrics — length in residual pool and mean maximum residual pool depth — provided useful measures of pool extent and quality and useful information on Chinook salmon habitat. Thalweg metrics differed between these undisturbed streams and reaches in streams affected by placer gold mining. These results suggest that thalweg profiling provides a useful tool to assess and monitor fish habitat in small streams.

Résumé : Les profils des thalwegs sont des profils longitudinaux de l'altitude du lit des cours d'eau mesurée le long de la plus grande profondeur. On a récemment prôné l'utilisation de cette technique comme outil d'évaluation et de surveillance des habitats de poissons dans les cours d'eau, parce que les métriques obtenues à partir des profils des thalwegs peuvent fournir des informations utiles sur la qualité de l'habitat et que ces mesures sont faciles à répéter et indépendantes du débit. On connaît aussi les relations entre les métriques des thalwegs et l'utilisation des terres. Personne n'a cependant établi de relation entre les métriques des thalwegs et l'abondance des poissons. Dans le but de mettre au point une telle relation, nous avons inventorié les profils des thalwegs et les densités de jeunes saumons chinook (*Oncorhynchus tshawytscha*) dans 14 sections de petits tributaires du cours supérieur du fleuve Yukon. Il y a une corrélation entre la densité du saumon chinook et trois métriques des thalwegs. Deux de ces métriques — la longueur des fosses résiduelles et la profondeur maximale moyenne des fosses — fournissent des mesures utiles de l'importance et de la qualité des fosses et des données pratiques sur l'habitat du saumon chinook. Les métriques des thalwegs diffèrent entre ces cours d'eau non perturbés et des sections de cours d'eau affectées par l'exploitation minière de placers aurifères. Nos résultats indiquent que les profils des thalwegs sont un outil commode pour l'évaluation et la surveillance de l'habitat des poissons dans les petits cours d'eau.

[Traduit par la Rédaction]

Introduction

Methods to assess and monitor habitat in streams are important tools for managing fish and their habitat because it is generally easier to measure habitat variables than it is to estimate fish abundance. Furthermore, abundance can vary in response to factors unrelated to habitat (e.g., prey abundance). Interest in predicting fish yield from streams is evident by the number and diversity of existing habitat models (see reviews in Fausch et al. 1988; Shirvell 1989; Rosenfeld 2003) and corresponding habitat assessment and monitoring techniques (reviewed in Bain and Stevenson 1999). These methods are used to measure habitat change, assess environmental impacts, predict the benefits of enhancement projects, and determine flows in regulated rivers.

A fundamental problem in monitoring fish habitat is the lack of standardized, systematic approaches to collect data (Bauer and Ralph 2001). For example, habitat models that predict salmonid standing crop in streams (e.g., number or biomass of fish per unit of stream area) using physical habitat variables such as wetted area, substrate, or cover can be useful for predicting changes to fish habitat and fish populations.

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However, these models often use physical habitat variables that are dependent on stream flow (i.e., pool size and depth) or variables that are difficult to define objectively (i.e., cover; boundaries between pools, glides, and riffles). Consequently, these variables are difficult to measure consistently, thereby limiting the utility of such models for management (Poole et al. 1997), especially for long-term monitoring where different field crews are involved. Monitoring is an important component of adaptive management programs, and effective monitoring of aquatic habitats has received growing attention from resource managers and scientists (Kaufmann et al. 1999; Roper et al. 2002; Larsen et al. 2004).

Bauer and Ralph (2001) outline the characteristics of effective monitoring techniques and measurement variables for stream habitat. They suggest that monitoring should be (*i*) relevant to the biotic endpoint, including a quantifiable relation; (*ii*) responsive to management impacts; (*iii*) appropriate to the stream network; and (*iv*) measured with acceptable precision and accuracy. The habitat-monitoring tools they reviewed failed to meet at least one of these criteria, frequently criteria *i* and *iv*.

Thalweg profiling has been advocated as a useful tool to assess and monitor fish habitat in small streams, in part because it can improve the accuracy and precision of channel and pool measurements (e.g., Bauer and Ralph 2001). Thalweg profiling involves surveying the streambed elevation along the deepest portion of the stream (the thalweg) to produce a two-dimensional, longitudinal profile of streambed elevations. Depressions in the profile represent pools or deeper habitats with low velocity during low flow periods, while crests in the profile represent riffles. Metrics calculated from thalweg profiles can provide quantitative measures of stream channel morphology that are relevant to fish. For example, residual pool depth, equal to the difference between the elevation of the deepest point in a pool and the elevation of the riffle crest immediately downstream (Lisle 1987), is commonly used in stream habitat assessment and monitoring to index potential pool habitat, independent of flow.

Thalweg profiling has long been used to study stream channel morphology (e.g., Richards 1976). Thalweg profiling is also used in stream habitat assessment and monitoring (MacDonald et al. 1991; Bain and Stevenson 1999), including the design and monitoring of habitat restoration projects (Newbury and Gaboury 1993). For instance, the United States Environmental Protection Agency's Environmental Monitoring and Assessment Program has measured thalweg profiles repeatedly for thousands of small streams (Kaufmann et al. 1999). Recent studies on fish habitat and channel morphology have suggested calculating metrics from the profile that would provide useful indices of fish habitat (Lisle 1995; Madej 1999*a*). For example, Madej (1999*b*) suggested using an index of morphological diversity to monitor channel conditions based on the assumption that a more variable morphology reflects more complex aquatic habitat and, therefore, better fish habitat. However, the relation between fish populations and such thalweg metrics has not been examined. Therefore, the utility of thalweg profiling for assessing and monitoring fish habitat has yet to be tested, as per criterion *i* of Bauer and Ralph (2001).

This study evaluates thalweg profiling as a tool to monitor fish habitat in small streams. Our objectives were (*i*) to determine whether metrics of channel structure calculated from thalweg profiles provide good measures of fish habitat and are good predictors of fish abundance and (*ii*) to determine whether these metrics are suitable for monitoring the impacts of placer mining. We first determine whether there is a relation between the abundance of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and thalweg metrics in small, undisturbed tributary streams of the upper Yukon River in northern Canada. We then compare thalweg metrics from these undisturbed streams with nearby streams that have been placer-mined for gold to determine whether these metrics reflect the impacts of land use on channel morphology. We also describe methods for thalweg profiling as applied in the context of fish habitat monitoring.

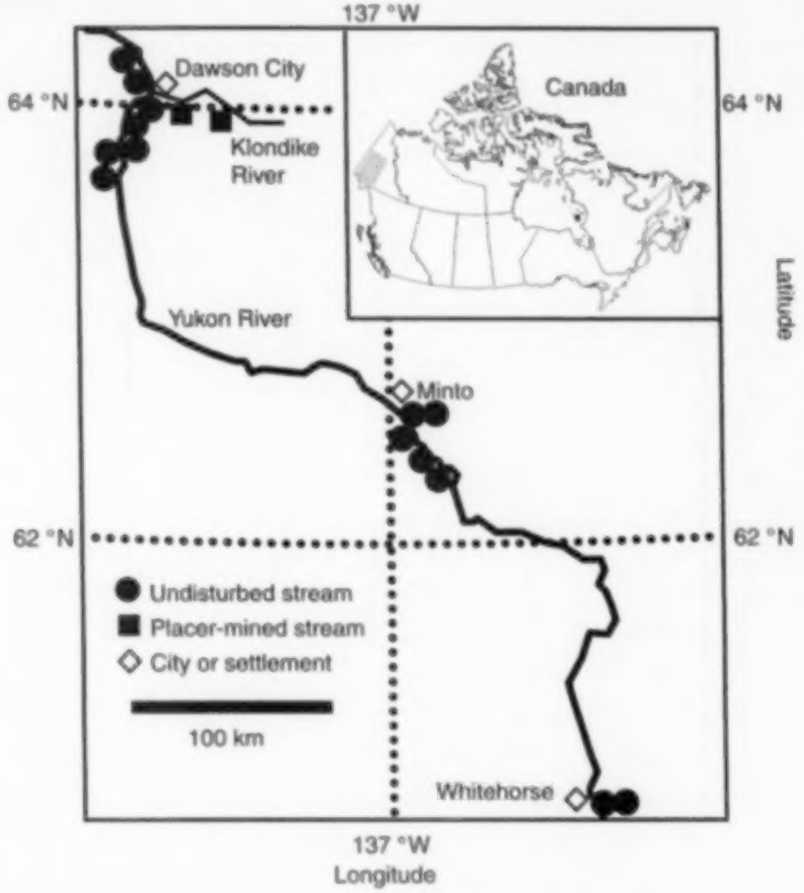
The Yukon River is an important producer of Chinook salmon, and juvenile Chinook salmon make extensive use of small streams in the Yukon River Basin (Bradford et al. 2001). Adult Chinook salmon spawn in the Yukon River mainstem and large tributaries in the fall. Small nonnatal streams are colonized the following June and early July by juvenile (age-0) Chinook salmon that migrate downstream from spawning areas (Bradford et al. 2001). In these small streams, juvenile Chinook salmon densities were found to be several times higher in pools and deeper habitats and generally less abundant or absent in habitat units <25 cm deep (Bradford et al. 2001). During late July, median densities in pools, glides, and riffles in an intensively studied stream were 3.4, 0.4, and 0.0 fish·m^{-2}, respectively. While habitat selection by stream-rearing salmonids and the associated fitness consequences of habitat use likely involve complex interactions among energetic costs and benefits, competition, and risk of predation (Rosenfeld 2003), higher abundance, survival, and (or) growth in deeper pool habitats is commonly reported for many species of juvenile salmonids (e.g., Lonzarich and Quinn 1995; Rosenfeld and Boss 2001). Given this habitat selection in Yukon streams, we hypothesized that more juveniles would colonize streams with better-quality habitat; specifically, streams with more abundant deep pools. Therefore, we also hypothesized that reach-scale Chinook salmon density would be positively related to thalweg metrics that quantified pool habitat, such as residual pool depth.

Materials and methods

Study area and habitat conditions

We examined 12 relatively undisturbed and two actively placer-mined small tributary streams to the upper Yukon River (Fig. 1). Placer mining refers to the recovery of fine gold from alluvial deposits and frequently involves diverting the stream prior to removing, processing, and redepositing the valley bottom and stream channel (LaPerriere and Reynolds 1997). Streams were grouped into three subregions of the Yukon Territory, Canada: Whitehorse, Minto, and Dawson City (Fig. 1). The topography of the stream valleys differed among subregions. The Dawson subregion was not glaciated during the last glacial maxima of 40 000 to 14 000 years before present (1950) (Oswald and Senyk 1977); consequently, the stream valleys were more steeply incised. In contrast, the previously glaciated stream valleys near Minto and Whitehorse had a more gentle topography. Croucher Creek near

Fig. 1. Map of the Yukon River and study sites. Study streams are direct tributaries to the Yukon River or Klondike River, and the drainage areas for these small streams would be slightly larger than the points that indicate their locations. Inset highlights location in the Yukon Territory, Canada.



Whitehorse has incised into sediments deposited in ancient glacial lakes and rivers.

Boreal forest dominated by white spruce (*Picea glauca*) covers the valley bottoms of these streams (described in Mossop and Bradford 2004). Discontinuous permafrost is found throughout the region (Oswald and Senyk 1977). Stream discharge is characterized by peak flows in June caused by snow and ice melt, followed by base flows and occasional spates following thunderstorms during the summer (Woo 1986). Smaller streams are covered with 1–3 m of ice during the winter (Bradford et al. 2001) and may freeze solid to the channel bed.

Streams that we surveyed are direct tributaries to the Yukon River mainstem, with the exception of the two placer-mined streams that flow into the Klondike River, a large tributary of the Yukon River. All streams were second- to fourth-order (at the 1:50 000 scale) and had pool–riffle or plane-bed morphology (Montgomery and Buffington 1998; Table 1). Streambeds were alluvial and some of the plane-bed streams had areas with exposed bedrock. Substrate was predominantly gravel (2 to 64 mm) and cobble (65 to 256 mm), with relatively larger substrate in steeper streams. Croucher Creek had smaller substrate, with sand in pools and gravel and small cobble in riffles.

Juveniles colonizing from the mainstem generally spend their first summer in these small tributary streams and may overwinter in areas where flows are adequate. In August, most juvenile Chinook salmon are age-0 (mean fork length = 65 mm), although a few age-1 Chinook salmon may also be present (Bradford et al. 2001). Juvenile Chinook salmon dominate the fish community in these streams, although Arctic grayling (*Thymallus arcticus*), slimy sculpin (*Cottus cognatus*), longnose sucker (*Catostomus catostomus*), lake chub (*Couesius plumbeus*), and juvenile northern pike (*Esox lucius*) are also present (Bradford et al. 2001), and nonnative rainbow trout (*Oncorhynchus mykiss*) occur in Croucher Creek.

These streams are an ideal model system for testing the relation between physical habitat and fish abundance because physical habitat structure, rather than biological factors such as recruitment, predation, or interspecific competition, likely limits abundance. Recruitment of juveniles does not appear to limit abundance in individual streams because there is no spawning in these streams, and streams are colonized by a large pool of juvenile Chinook salmon moving in from the

Table 1. Physical and biological data for 14 undisturbed and two placer-mined stream reaches.

Stream	Location	Gradient (%)	Bank-full width (m)	Drainage area (km^2)[a]	Channel type[b]	Water temperature (°C)	Conductivity ($\mu S \cdot cm^{-1}$)	Riparian canopy cover (%)	Large woody debris abundance ($no. \cdot 100m^{-1}$)[c]	Chinook salmon density ($no. \cdot m^{-2}$)
Undisturbed streams										
Croucher (upper)	Whitehorse	1.1	4.6	122	pr	10.6	282	92	78.0	0.49
Croucher (lower)	Whitehorse	1.3	5.7	123	pr	10.6	282	89	70.6	0.41
Hoocheekoo	Minto	0.7	4.5	85	pr	5.7	414	87	39.8	2.26
McCabe (upper)	Minto	0.7	5.6	193	pr	6.4	386	62	24.5	2.42
McCabe (lower)	Minto	0.9	5.0	197	pr	6.5	377	90	12.6	0.41
Merrice	Minto	1.9	5.5	136	pb	5.2	226	94	10.3	0.13
Williams	Minto	1.2	5.3	91	pr	5.3	349	95	22.3	1.14
Baker	Dawson	3.6	5.2	26	pb	6.0	314	52	21.3	0.26
Caribou	Dawson	4.2	3.4	18	pb	5.0	386	88	4.9	0.05
Deadwood	Dawson	3.1	4.2	30	pb	4.7	474	89	13.5	0.11
Ensley	Dawson	1.3	5.4	74	pr	6.7	355	91	25.2	0.84
Garner	Dawson	1.3	4.7	73	pr	5.7	250	66	35.2	1.01
Mechem	Dawson	2.0	4.7	59	pr	5.4	305	82	37.7	0.98
Quebec	Dawson	2.1	4.8	37	pb	5.0	170	70	13.0	0.03
Placer-mined streams										
Bonanza	Dawson	1.0	11.1	206	pb	—	—	—	—	—
Hunker	Dawson	0.8	6.2	93	pb	—	—	—	—	—

Note: Bank-full width and channel type are not "natural" for placer-mined streams and thus are not directly comparable with undisturbed streams.

[a] Area upstream of sampled reach.

[b] Channel type from Montgomery and Buffington (1998): pr, pool–riffle; pb, plane-bed.

[c] Data from Mossop and Bradford (2004).

Table 2. Thalweg metrics for 14 undisturbed and two placer-mined stream reaches.

Stream	Location	Variation index	Mean square error	Length in residual pool (proportion)	Mean max residual pool depth (m)
Undisturbed streams					
Croucher (upper)	Whitehorse	0.14	0.028	0.73	0.30
Croucher (lower)	Whitehorse	0.16	0.031	0.72	0.28
Hoocheekoo	Minto	0.15	0.027	0.80	0.46
McCabe (upper)	Minto	0.17	0.039	0.68	0.38
McCabe (lower)	Minto	0.19	0.041	0.77	0.41
Merrice	Minto	0.07	0.030	0.05	0.27
Williams	Minto	0.17	0.039	0.57	0.35
Baker	Dawson	0.05	0.016	0.05	0.16
Caribou	Dawson	0.03	0.011	0.05	0.14
Deadwood	Dawson	0.07	0.030	0.11	0.19
Ensley	Dawson	0.10	0.020	0.48	0.26
Garner	Dawson	0.10	0.018	0.58	0.24
Mechem	Dawson	0.08	0.024	0.34	0.23
Quebec	Dawson	0.04	0.021	0.12	0.12
Mean		0.11	0.027	0.43	0.27
CV (%)		49	34	69	38
Placer-mined streams					
Bonanza	Dawson	0.03	0.003	0[a]	0[a]
Hunker	Dawson	0.06	0.017	0.42	0.17
Mean		0.04	0.010	0.21	0.08
CV (%)		55	98	NA	NA

Note: Thalweg metrics are defined in the text and are based on measurements made in metres. CV, coefficient of variation; NA, not applicable.

[a] No pools with a residual depth >0.1 m deep were present in Bonanza Creek.

Yukon River mainstem. We interpret our results to suggest that, for a given length of stream, more juveniles colonize streams with better quality Chinook salmon habitat, such as deep pools.

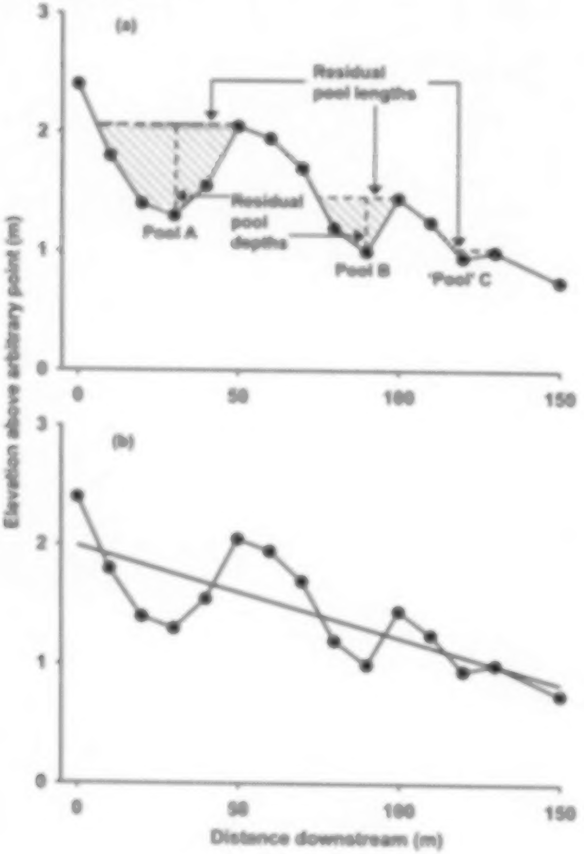
Although these watersheds were relatively undisturbed by recent human activities, many were logged to fuel steamboats that navigated the Yukon River in the 1890s–1950s. No detailed records are available for the fire history or the exact timing and extent of such logging in individual watersheds. Valley bottoms of the two mined streams (Hunker and Bonanza creeks) have been placer-mined repeatedly throughout much of their length since the Klondike gold rush of the 1890s. Placer mining is an extreme disturbance to the stream channel. Streams were diverted while the underlying gold-bearing gravels were mined using techniques that ranged from hand-mining to mechanized dredging to extract and process deposits. Placer mines were active in both watersheds when we surveyed them.

Study design

We surveyed thalweg profiles and sampled juvenile Chinook salmon densities from reaches of undisturbed (i.e., not placer-mined) streams with known presence of juvenile Chinook salmon. Stream selection was dictated largely by access; we sampled all small streams that were potentially useable for salmon near Minto and Dawson (Fig. 1) and one stream with road access near Whitehorse. We surveyed one reach on 10 of the 12 undisturbed streams and two separate reaches on each of the remaining two undisturbed streams for a total of 14 reaches. We use the term stream reach to refer to a specified stream length within a longer, geomorphologically homogeneous reach. All reaches were ≥18 bank-full channel widths long (84–190 m). Reaches were surveyed near the stream's confluence with the Yukon River, with the exception of the upper reach on McCabe Creek (3 km upstream of the Yukon River) and both reaches on Croucher Creek (1.0 and 1.5 km upstream of the Yukon River). We chose reaches near the stream's confluence with the Yukon River to maximize the likelihood that the reach would be fully colonized by salmon. Thalweg surveys took place from late June to early August 2001, while Chinook salmon densities were sampled in August over several years, as described below.

We compared thalweg metrics from undisturbed streams and two actively placer-mined streams. We surveyed Bonanza and Hunker creeks roughly 9 and 14 km, respectively, upstream from their confluence with the Klondike River. We did not sample fish in these mined reaches because differences in Chinook salmon density between mined and undisturbed streams may be attributed to factors unrelated to physical habitat structure. The abundance of juvenile Chinook salmon in the Klondike River is lower than that in the Yukon River mainstem (M.J. Bradford, unpublished data), and high suspended sediment loads discharged from active placer mines may discourage colonization. These factors potentially violate our assumption that salmon densities were limited by physical habitat structure.

Fig. 2. Hypothetical thalweg profiles to illustrate calculations for the thalweg metrics. Profile (*a*) highlights residual pools. Pools A and B meet the 0.1 m minimum depth criterion. 'Pool' C illustrates a small morphological feature that is shallower than the minimum depth criterion and, therefore, is not included in the calculations for the thalweg metrics length in residual pool or mean maximum residual pool depth. Profile (*b*) illustrates a linear regression line fit to the thalweg data. The thalweg metric mean square error, an index of profile variability, is calculated from this regression.



Chinook salmon densities

We used published estimates of reach-scale juvenile Chinook salmon densities that were collected using either two-pass depletion electrofishing or mark–recapture methods (Mossop and Bradford 2004). Reaches were sampled in August from 1998 to 2002, though logistical challenges limited sampling of each reach in a given year. Since Chinook salmon densities varied nearly 100-fold among reaches (Table 1) and these differences among reaches were consistent between years (Mossop and Bradford 2004), we used densities averaged across years (arithmetic means for each reach) to reduce the effects of natural variation and sampling error (Mossop and Bradford 2004).

Thalweg profiling

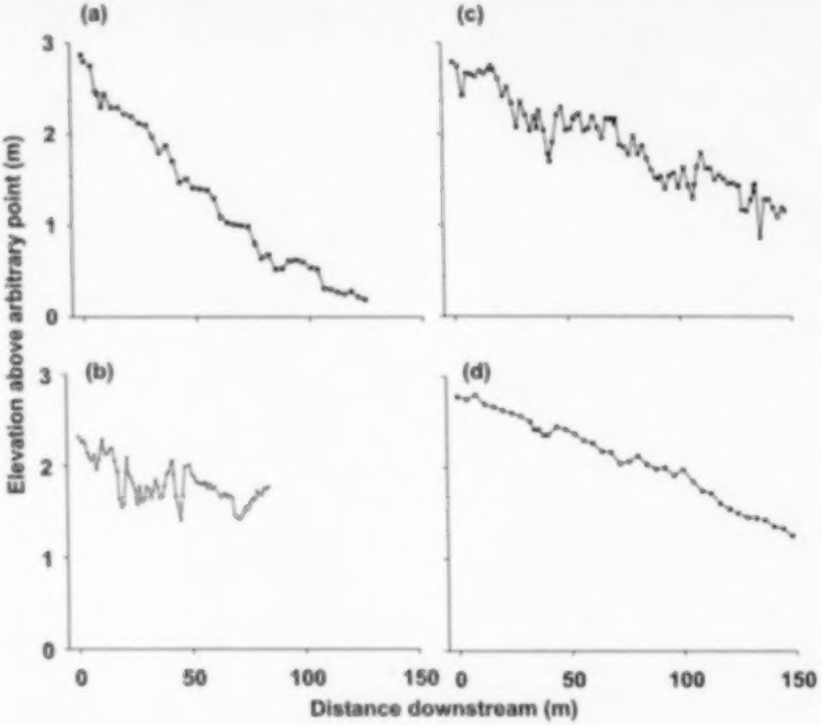
We surveyed thalweg profiles using standard surveying techniques (Harrelson et al. 1994) and the thalweg survey methods described in Madej (1999*a*). We used a three-person crew consisting of a surveyor, rod person, and data recorder. On average, this crew surveyed a 150 m reach in 3 h. Surveys began and ended at riffle crests (the location in a riffle with the highest elevation) for streams with a pool–riffle structure or ended mid-riffle for streams lacking pool–riffle morphology. Streambed elevation at the channel thalweg was measured using a survey level and stadia rod at a systematic interval every 0.25–1.0 bank-full width (1–5 m), as well as at every break in streambed slope. Interval width was adjusted to bed morphology such that reaches with more variable bed morphology were sampled using a shorter interval. The stadia rod had a 52 mm × 30 mm base. The rod was supported to prevent it from sinking into the smaller, softer substrates at Croucher Creek. Distance along the channel was referenced to a tape that ran as straight as possible along the channel.

Numerous metrics can be calculated from a thalweg profile. We examined two groups of metrics: those that directly measure (*i*) pool abundance and characteristics and (*ii*) variability of the profile. Pools that would be present during low flow periods are represented as depressions in the thalweg profile. Such depressions can be measured by the residual pool depth (Fig. 2*a*). Residual pool depth represents the depth of a pool that would theoretically remain if there were no flow in the stream (Lisle 1987). As more than one streambed elevation can be measured along a residual pool (e.g., the four streambed elevations that form the bottom of Pool A in Fig. 2*a*), we refer to residual depth as any residual depth measured along a residual pool; maximum residual pool depth is the maximum residual depth in a pool.

We examined metrics of both pool extent and residual pool depth, because we expected Chinook salmon to respond to both pool abundance and depth (quality). "Length in residual pool" (Lisle 1986) represents pool abundance or extent and is expressed as the proportion of the stream length in residual pools, calculated as the total length of all stream sections in residual pools (e.g., the length of Pools A and B in Fig. 2*a*) divided by the surveyed reach length. "Mean maximum residual pool depth" is an index of pool quality and is calculated as the average of the maximum residual pool depths in a reach. We applied a minimum residual depth criterion of ≥0.1 m to these two metrics to ensure that residual depths reflected major morphological features and not small irregular features in the streambed (e.g., 'Pool' C in Fig. 2*a*). Further, Chinook salmon in these streams were most abundant in habitat units >0.25 m deep (Bradford et al. 2001), which was equivalent to pools and glides with residual depths greater than ~0.1 m.

We examined two metrics of profile variability: one of variation within pools and another of variation within the reach. The "variation index" (Madej 1999*a*) is an index of variation within pools that is calculated as the standard deviation of the population of residual depths along the reach. Higher variation index values indicate more variable morphology within residual pools. Unlike Madej (1999*a*), we did not standardize this metric to account for differences in stream size because we surveyed a relatively small range of channel sizes (Table 1), and our purpose was to develop metrics to monitor changes in a given stream over time. "Mean

Fig. 3. Thalweg profiles for three undisturbed stream reaches (*a*–*c*) and one placer-mined reach (*d*). (*a*) Quebec Creek, (*b*) Hoocheekoo Creek, (*c*) Croucher Creek (upper), (*d*) Bonanza Creek.



square error" (MSE) is another index of profile variability, which is calculated as the MSE from a linear regression line fit to the thalweg data (Fig. 2*b*). Higher MSE values should represent more variable profiles. Channel gradient generally decreases as one moves downstream at the watershed scale (Leopold et al. 1964), and a second-order polynomial fit to the thalweg data could account for such curvature in the profile. However, we found that a linear regression provided an adequate fit to our profiles because channel gradient was relatively constant along our relatively short reaches. We did not examine the numerous alternative measures of profile and residual pool variability because we did not have information on fish preference for pools or habitats with different bedform shapes with which to develop biologically based hypotheses and determine the features that the metrics should quantify. Further, our reach-scale approach did not provide fish abundance and bedform data at the scale of individual residual pools, which may be better suited to such tests.

We used correlation analysis to compare Chinook salmon density with each thalweg metric. The habitat features measured by thalweg metrics are the result of geomorphic processes that depend on other stream attributes. Therefore, to help understand the relation between thalweg metrics and salmon abundance, we included two other variables related to physical habitat for which we had data: average stream gradient and the abundance (pieces·100 m^{-1}) of large woody debris (LWD; data from Mossop and Bradford 2004). We also assessed the collinearity among thalweg metrics, gradient, and LWD abundance. Where appropriate, variables were $\log_{10}$-transformed to standardize variances and improve normality.

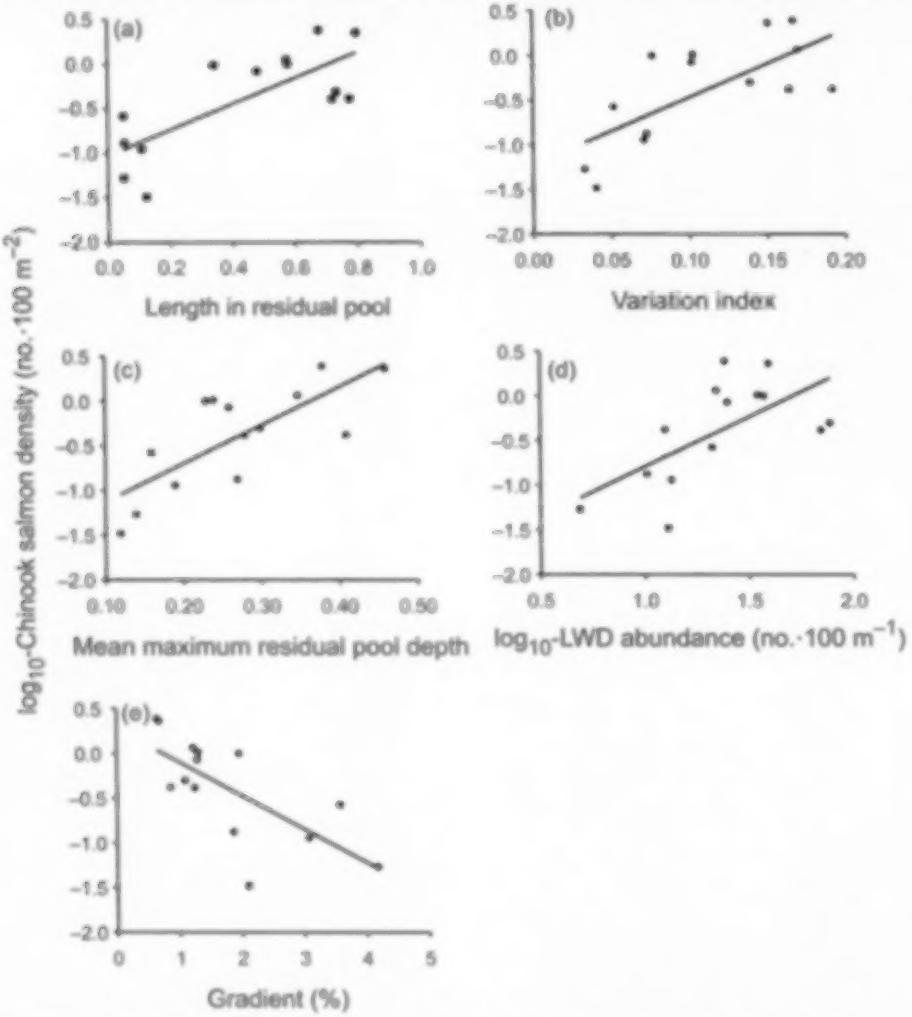
Our correlative approach to examine the relation between Chinook salmon density and thalweg metrics assumes that other biological characteristics of the streams that could influence fish abundance do not systematically covary with thalweg metrics, potentially confounding our results. We collected data on water conductivity, water temperature, and percent riparian canopy cover (Table 1) that could serve as surrogates for primary and secondary productivity and found that none were related to either fish density or thalweg metrics (all $P > 0.05$; $n = 14$ for canopy cover; $n = 12$ for analyses with water quality parameters, since for Croucher and McCabe creeks we used average values for the upper and lower reaches). Our purpose here was to support the inferences that could be drawn from potential correlations between Chinook salmon density and thalweg metrics and not to determine the factors that drive juvenile salmon abundance in these streams, as these factors are well documented in other systems (see summary in Fausch et al. 1988).

Results

Thalweg profiles and metrics in undisturbed reaches

Differences among thalweg profiles are qualitatively apparent in the example profiles in Fig. 3. Quebec Creek (Fig. 3*a*) is typical of steeper gradient reaches with straight, uniform profiles. Hoocheekoo Creek (Fig. 3*b*) is typical of lower-gradient reaches with more variable or bumpier profiles.

Fig. 4. Correlation between juvenile Chinook salmon (*Oncorhynchus tshawytscha*) density and selected thalweg metrics and habitat variables from 14 stream reaches. All correlations are significant ($P < 0.05$); correlation coefficients are provided in Table 3.



Croucher Creek (upper) (Fig. 3*c*) is intermediate between these two. Thalweg metrics provide a quantitative representation of these qualitative differences between profiles. All metrics except MSE were highest in Hoocheekoo Creek, intermediate in Croucher Creek (upper), and lowest in Quebec Creek (Table 2). The MSE values were less consistent with qualitative differences seen in the profiles; values were higher in Croucher Creek (upper) than in Hoocheekoo Creek and were lowest in Quebec Creek.

Values for all thalweg metrics varied at least fourfold among the undisturbed reaches (Table 2). The coefficient of variation (across all undisturbed reaches) for length in residual pool (69%) was higher than for those of the other three metrics (34%–49%; Table 2). The distribution of length in residual pool was notably clustered into values ≤0.12 and ≥0.34 (Table 2; Fig. 4*a*), which corresponds with the observed plane-bed and pool–riffle channel morphologies (Table 1).

Thalweg metrics were positively correlated with each other, and they all decreased with increasing channel gradient in the undisturbed streams (Table 3). The latter trend is apparent in Figs. 3*a*–3*c*, as steeper streams had less variable profiles with fewer residual pools.

Chinook salmon density and thalweg metrics

Chinook salmon densities varied greatly among reaches (Table 1), and thalweg metrics explained up to 57% of the variation in the $\log_{10}$-transformed data (Fig. 4; Table 3). Log_{10}-Chinook salmon density was strongly correlated with three of the four thalweg metrics, the exception being MSE. Log_{10}-Chinook salmon density was also positively correlated with $\log_{10}$-LWD abundance and negatively correlated with channel gradient (Fig. 4; Table 3).

Thalweg profiles and metrics in mined streams

Thalweg profiles for the two mined reaches were less variable than those for undisturbed streams of similar gradient. Bonanza Creek (Fig. 3*d*) had a uniform profile despite having a low gradient, similar to Croucher Creek (upper)

Table 3. Pairwise correlation coefficients among thalweg metrics, habitat variables, and Chinook salmon (*Oncorhynchus tshawytscha*) density in 14 stream reaches.

	Gradient	$\log_{10}$-Chinook salmon density	$\log_{10}$-LWD abundance	Mean square error	Mean max residual pool depth	Length in residual pool
$\log_{10}$-Chinook salmon density	−0.71	—				
$\log_{10}$-LWD abundance	−0.60	0.64	—			
Mean square error	−0.66	0.42	0.19	—		
Mean max residual pool depth	−0.81	0.76	0.37	0.73	—	
Length in residual pool	−0.86	0.76	0.67	0.56	0.83	—
Variation index	−0.83	0.70	0.50	0.81	0.89	0.92

Note: Light shading represents $r > 0.55$ and $P < 0.05$; dark shading represents $r < -0.55$ and $P < 0.05$; and no shading represents $P > 0.05$. LWD, large woody debris.

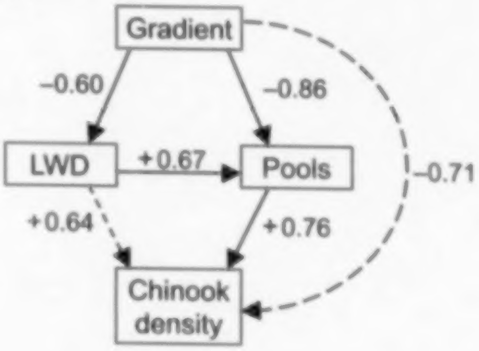
(Fig. 3c), which had a more variable profile. Thalweg metrics for the two mined reaches were, on average, roughly one-third of values for undisturbed reaches of similar gradient (Table 2).

Discussion

The main result of this study is that thalweg profiles can provide useful information on fish habitat. Unlike previous thalweg profiling studies, we further related fish density to thalweg metrics and showed that juvenile Chinook salmon density was correlated with thalweg metrics. Quantifying these relations is an important step in validating thalweg profiling as a tool to assess and monitor fish habitat. Previous thalweg profiling studies have shown that thalweg profiling measures habitat features that (*i*) are responsive to management impacts (e.g., Hogan 1987); (*ii*) may be measured at the reach scale with acceptable precision and accuracy (Madej 1999*a*; Keim and Skaugset 2002); and (*iii*) are common to streams over a broad geographic area. Our results demonstrate a quantifiable relation between thalweg metrics measured at the reach scale and fish abundance. Given this relation, thalweg profiling can meet the four criteria for effective monitoring techniques of Bauer and Ralph (2001). Together, these results suggest that thalweg profiling is a useful tool to monitor fish habitat in Yukon streams and can also likely be adapted to monitor fish habitat in other regions.

The range of channel gradients sampled provided the contrast in channel morphology, and hence thalweg profiles, that were needed to test for relations between Chinook salmon density and thalweg metrics. Potential differences in sediment supply across the broad geographic area sampled may have provided additional contrast in channel morphology. Stream channel morphology and habitat complexity are influenced by the geologic setting and resulting topography of the watershed (as it affects channel gradient), as well as by sediment supply and in-stream obstructions such as LWD and boulders. In the Yukon, steeper gradient streams had less variable profiles and fewer residual pools than lower-gradient streams. This result is consistent with geomorphic theory. Pool–riffle morphology generally occurs at gradients less than ~2%, and a more featureless plane-bed morphology is found in steeper streams (Montgomery and Buffington 1998). LWD was also more abundant in lower-gradient streams and exerted a greater influence on the morphology of lower-gradient channels (Mossop and Bradford 2004). Thus, channel gradient drives changes in channel morphology and physical habitat, such as pool habitat and LWD abundance. These aspects of physical habitat (and not channel gradient itself) are important for juvenile Chinook salmon. Indirect correlations between channel gradient and Chinook density are most likely mediated by direct correlations with pools and LWD (Fig. 5).

Fig. 5. Hypothesized overall physical control of channel gradient on physical habitat features and, consequently, juvenile Chinook salmon (*Oncorhynchus tshawytscha*) densities. LWD is large woody debris abundance; pools refers to the thalweg metric length in residual pool. Shown are correlation coefficients (all $P < 0.05$; LWD abundance and Chinook density were $\log_{10}$-transformed). Solid lines represent likely direct effects and broken lines represent indirect effects. LWD affects Chinook salmon density either directly (i.e., LWD provides cover) or indirectly by forming pool habitat.



Chinook salmon density was correlated with three thalweg metrics: length in residual pool, mean maximum residual pool depth, and the variation index. Pools are important salmon habitat in the Yukon River Basin (Bradford et al. 2001), and length in residual pool and mean maximum residual pool depth provide direct measures of pool extent and quality. While the variation index was designed as an index of profile variability (Madej 1999*a*), it essentially only measures variation within residual pools or residual pool shape. It also indirectly provides an index of pool depth because variation is correlated with the mean (i.e., deeper pools produce higher variation index values; Madej 1999*a*; this study). Consequently, the correlation between Chinook salmon density and the variation index may be attributable to this metric's indirect measurement of pool depth rather than the variation in residual depths. Given this alternative explanation, the correlation between Chinook salmon density and the variation index does not necessarily support the assumption of Madej (1999*b*) that a more variable morphology reflects better habitat for fish.

Chinook salmon density was not correlated with MSE, possibly because this metric does not measure available pool habitat. Unlike the other metrics, MSE is not based on residual pools but is the mean of the squared residuals above or below a linear regression line. Our data illustrate that profiles with only a few shallow residual pools can have similar deviations from the regression line at the reach scale as profiles with extensive and deep residual pools. For example, Deadwood Creek was a steep plane-bed stream with few residual pools and had low Chinook salmon density. Deadwood Creek had a low variation index, length in residual pool, and mean maximum residual pool depth, yet had a high MSE, similar to streams with extensive deep pools.

Mined streams had lower thalweg metrics than undisturbed streams of similar gradient. As Chinook salmon density is correlated with thalweg metrics, we infer that Chinook salmon habitat in these mined streams was inferior to habitat in undisturbed streams of similar gradient. While this comparison is provisional because we only surveyed two placer-mined streams, it is consistent with previous studies on the relation between pool characteristics and land use (Gilvear et al. 1995; Wood-Smith and Buffington 1996; Kershner et al. 2004). Thalweg profiling would be an effective tool to monitor geomorphological recovery and the subsequent recovery of fish habitat after placer mining stops.

Based on our results in Yukon streams, we recommend using both length in residual pool and mean maximum residual pool depth to assess and monitor habitat for pool-rearing juvenile salmonids in small streams. Similar to other methods that monitor pool characteristics, thalweg profiling is best suited to monitor lower-gradient pool–riffle channels that are responsive to changes in sediment supply or peak flows and where pools span the channel (MacDonald et al. 1991; Montgomery and Buffington 1998; Montgomery and MacDonald 2002). It may be more challenging to develop thalweg metrics that provide useful measures of habitat for species with habitat preferences that differ from those of pool-rearing juvenile salmonids examined here. We calculated measures of residual pools that successfully measured the habitat preferences of juvenile Chinook salmon in the Yukon because these fish are abundant in deep pools. Metrics that measure pool extent and abundance may not be suitable for species that rear in riffles, although other metrics could be calculated for such species.

In summary, the major advantage of using thalweg profiling to assess and monitor fish habitat relative to other techniques is that measurements are repeatable and independent of stream flow, and the technique is relatively simple, rapid, and inexpensive to apply (this study; MacDonald et al. 1991). Thalweg profiles are well suited to monitor channel features such as residual pool depth and frequency, which have become favoured monitoring indices because they are (*i*) commonly agreed upon as important to salmonids; (*ii*) frequently targeted for restoration activities and improved management practices; and (*iii*) a sensitive indicator to detect changes over time (summarized in Larsen et al. 2004). The relation we document between Chinook salmon density and measures of residual pools supports the growing literature on residual depth. Thalweg profiles provide a good measure of physical habitat, and thalweg profiling can be incorporated as a central component of a more comprehensive program to monitor fish habitat.

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Interactions of slimy sculpin (*Cottus cognatus*) with native and nonnative trout: consequences for growth

Julie K.H. Zimmerman and Bruce Vondracek

Abstract: We examined growth of native slimy sculpin (*Cottus cognatus*), native brook trout (*Salvelinus fontinalis*), and nonnative brown trout (*Salmo trutta*) to investigate potential interactions of a native nongame fish with native and nonnative trout. Enclosures (1 m^2) were stocked with five treatments (juvenile brown trout with sculpin, juvenile brook trout with sculpin, and single species controls) at three densities. Treatments (with replication) were placed in riffles in Valley Creek, Minnesota, and growth rates were measured for six experiments. We examined the difference in growth of each species in combined species treatments compared with each species alone. We did not find evidence of interactions between brook trout and sculpin, regardless of density or fish size. However, sculpin gained greater mass when alone than with brown trout when sculpin were >16 g. Likewise, brown trout grew more when alone than with sculpin when brown trout were >24 g. In contrast, brown trout ≤5 g grew more with sculpin compared with treatments alone. We suggest that native brook trout and sculpin coexist without evidence of competition, whereas nonnative brown trout may compete with sculpin.

Résumé : Nous étudions la croissance du chabot visqueux (*Cottus cognatus*) indigène, de l'omble de fontaine (*Salvelinus fontinalis*) indigène et de la truite brune (*Salmo trutta*) non indigène afin de déterminer les interactions potentielles entre un poisson sportif indigène avec des salmonidés, l'un indigène et l'autre non indigène. Nous avons empoissonné des enclos (1 m^2) selon cinq combinaisons (jeunes truites brunes et chabots, jeunes ombles de fontaines et chabots et témoins des trois espèces isolées) à trois densités différentes. Les expériences (en double) ont été conduites dans des zones rapides de Valley Creek, Minnesota; nous avons mesuré les taux de croissance dans six expériences. Nous avons calculé les différences de croissance de chaque espèce élevée en compagnie d'une autre et élevée seule. Nous n'avons trouvé aucun signe d'interaction entre l'omble de fontaine et le chabot, quelles que soient les densités et les tailles des poissons. Cependant, lorsque les chabots ont une masse >16 g, ils atteignent des masses plus grandes seuls qu'en compagnie de truites brunes. De même, les truites brunes de masse >24 g croissent davantage seules qu'en présence de chabots. En revanche, les truites brunes ≤5 g croissent davantage en présence de chabots que seules. Nous pensons que les ombles de fontaines et les chabots indigènes cohabitent sans indication de compétition, alors que les truites brunes non indigènes peuvent entrer en compétition avec les chabots.

[Traduit par la Rédaction]

Introduction

Nonnative trout have been introduced around the world and have been implicated in changes in stream assemblages. Nonnative trout often possess superior competitive abilities (Fausch and White 1981), different reproductive strategies (Sorensen et al. 1995; Essington et al. 1998; Grant et al. 2002), different feeding behavior (Flecker and Townsend 1994; Townsend 1996; Biggs et al. 2000), greater physical and chemical tolerances, and use a broader range of habitat than native fauna (Waters 1983, 1999). Previous research has investigated competition between native and nonnative trout species (Fausch and White 1981, 1986; Sorensen et al. 1995) and effects of introduced trout on communities where native trout were not present (McIntosh and Townsend 1994; Dahl and Peckarsky 2002; Peckarsky et al. 2002). However, few

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studies have investigated effects of introduced trout on stream communities where native trout have been largely replaced by nonnative trout (but see Ruetz et al. 2003).

Successful introductions often have community-level effects on behavior and population densities of other species, with direct and indirect evolutionary consequences (Abrams 1996; Townsend 1996; Simon and Townsend 2003). Ecological impacts have been hypothesized to be due, in part, to a lack of co-evolution with native species (Simon and Townsend 2003). For example, brown trout (*Salmo trutta*) have been widely introduced and have been implicated in declines of brook trout (*Salvelinus fontinalis*) where brook trout are native (Waters 1999). Such changes in fish assemblages may alter interactions between species (e.g., increased competitive interactions between drift-feeding trout and benthic-feeding sculpin), potentially leading to evolutionary consequences. Although sculpin and trout often have similar diets (Petrosky and Waters 1975; Hesthagen et al. 2004), different feeding modes decrease the likelihood of direct competition for invertebrate prey (Moyle 1977). However, Ruetz et al. (2003) found interactions between nonnative brown trout and native slimy sculpin (*Cottus cognatus*) in Valley Creek, Minnesota, resulted in asymmetrical competition, with brown trout feeding in the drift and on benthic invertebrates and suppressing sculpin growth. Ruetz et al. (2003) did not investigate the relative effects of introduced brown trout and native brook trout on sculpin growth, nor potential changes in trout–sculpin interactions with changes in fish size and density. Although small coldwater streams are often numerically dominated by sculpin (Morgan and Ringler 1992), relative effects of introduced versus native trout on sculpin growth have not been investigated.

We examined interactions between slimy sculpin (a native benthic-feeder) and nonnative brown trout (primarily a drift-feeder) and interactions between slimy sculpin and native brook trout (a drift-feeder) in multiple experimental trials using different densities of each species. Our goal was to address the following question: How does replacement of native brook trout by nonnative brown trout affect growth and survival of a native nongame fish? Our objectives were to (*i*) examine growth and recovery rates (a surrogate for survival) of brook trout and slimy sculpin in single species and combined species treatments and (*ii*) compare the results of objective *i* with growth and recovery of brown trout and slimy sculpin in single species and combined species treatments. We hypothesized that brown trout would compete with and reduce sculpin growth, whereas competition would not occur between brook trout and sculpin. We did not expect slimy sculpin to reduce growth of either trout.

Materials and methods

Study site

We conducted our research in Valley Creek, a small (6 km) first- and second-order spring-fed stream in Washington County, Minnesota. The fish assemblage and production in Valley Creek is similar to other trout streams in the driftless area ecoregion of southeastern Minnesota, western Wisconsin, eastern Iowa, and northwestern Illinois. Streams in this area tend to be fertile, with relatively high alkalinity and conductivity, and may have high values of trout production (Kwak and Waters 1997). The entire length of Valley Creek is bordered by private land and has not been stocked with fish for at least 20 years (Sorensen et al. 1995). Mean water temperatures in our study reach ranged from 11.0 to 12.9 °C from mid-May to early September. The fish assemblage in Valley Creek mainly consists of native brook trout in the upper headwater reaches, introduced brown and rainbow trout (*Oncorhynchus mykiss*) in downstream reaches (Weigel and Sorensen 2001), and slimy sculpin throughout the stream. Density of trout ($\geq$9.0 cm) has been estimated as 0.5–0.6·m^{-2} (Weigel and Sorensen 2001), with highest mean trout density estimated at 0.7·m^{-2} (Waters 1999). Sculpin mean densities range from 1–6·m^{-2} in riffle habitats (Petrosky and Waters 1975; Ruetz et al. 2002, 2003). Valley Creek has been the subject of research for over 40 years, including a long-term study of trout production dynamics that documented the replacement of native brook trout by nonnative brown trout (e.g., Waters 1983, 1999).

Species interaction experiment

We designed a field experiment to examine interactions (growth and recovery) between sculpin and brook trout versus interactions between sculpin and brown trout, at different densities and sizes. We used a split-plot experimental design, with a split-plot factor of fish species treatment and a whole-plot factor of density. Fish species treatments included two combined species treatments (juvenile brown trout with sculpin, juvenile brook trout with sculpin) and three single species controls (brown trout alone, brook trout alone, sculpin alone). Fish density treatments were designed to examine the relative effects of interspecific versus intraspecific competition on fish species treatment effects rather than analyze effects of increasing the number of fish in enclosures.

We placed 1 m^2 enclosure–exclosure cages (hereafter enclosures; 1 m × 1 m × 0.75 m PVC frames with 6 mm mesh hardware cloth on four sides and bottom) in riffles in Valley Creek to use as the experimental unit for fish species treatments (the split-plot factor). Each riffle contained five enclosures. The five fish species treatments were randomly assigned to enclosures within each riffle, and fish species treatments were replicated among riffles in a randomized complete block. We distributed enclosures evenly throughout each riffle. Six replicates of each treatment were used for each experimental trial conducted during 2002 (i.e., each of six riffles contained all five fish species treatments), whereas nine replicates were used for trials conducted in 2003 and 2004. All fish were collected from Valley Creek in riffles adjacent to our study area.

Using a 1 m^2 template, we cleared substrate from the riffle until we had a relatively flat surface on which to place each enclosure. We placed two–three small boulders inside each enclosure to anchor it to the stream bottom and lined the entire bottom of each enclosure with substrate that had been previously cleared from the area. The substrate placed in enclosures comprised mainly gravel, cobbles, and small boulders. Although substrate in enclosures reflected substrate available in riffles, we were likely biased toward larger sizes, thus providing additional crevice space for fish.

Our three density designs included two additive designs (equal and unequal numbers of each species) and one substitutive design to examine the relative effects of interspecific versus intraspecific competition on fish growth, as suggested by Underwood (1986) and Fausch (1998). Density designs were randomly assigned to riffles in Valley Creek (riffles were the experimental unit for the whole-plot factor of density) within blocks of stream reach for each experimental trial. All fish densities used in our experiments approximated natural densities in the study stream. The unequal additive design reflected estimates of relative abundance for Valley Creek riffles: $1{\cdot}m^{-2}$ for trout and $3{\cdot}m^{-2}$ for sculpin (Table 1). The equal additive design used trout and sculpin densities of $3{\cdot}m^{-2}$ to avoid confounding different starting densities of each species with treatment effects (Underwood 1986; Ruetz et al. 2003). Our substitutive design kept total fish density constant at $4{\cdot}m^{-2}$ (with two fish of each species in combined treatments). Additive density designs (individuals of species B are added to a constant number of individuals of species A) are used to examine evidence for competition between species, whereas substitutive designs (individuals of species A are replaced by an equal number of individuals of species B) examine the relative strength of intra- versus inter-specific competition (Underwood 1986; Fausch 1998; Weber and Fausch 2003). With an additive design, competition is confounded with the increase in total fish density (Fausch 1988, 1998). Substitutive designs simultaneously reduce density of one species and add a competing species, potentially masking interspecific competition with intraspecific interactions (Underwood 1986). Using both designs allows an examination of the magnitude of competitive interactions between species, as well as the importance of adding another species relative to increases in density of the same species.

We conducted experimental trials three times during 2002, twice in 2003, and once in 2004, using different fish for each trial (Table 2). The duration of each trial was 40 days during 2002 and 38 days during 2003 and 2004. We collected age-1 trout to stock enclosures for experiments ending in June 2002, June 2003, and August 2002. We used age-0 trout for all experiments ending in mid-September 2002 and late August 2003 and 2004, because they had grown large enough (mean initial mass 4.3–12.8 g) to be retained by the 6 mm mesh of the enclosures. For each trial, we used sculpin that were approximately equal in length to trout when possible (mean initial length 7.2–8.6 cm; see Table 2 for initial mass of all three species for each trial).

We marked fish at the beginning of each trial by clipping the tip of one unique fin per individual of the same species to determine recovery and growth of individual fish over the duration of the experiment. We measured initial mass of all individuals at the beginning of each trial. At the end of each trial we collected all fish from the enclosures and again measured the mass of individuals to determine growth. Thus, we defined growth as change in mass over each trial.

During each trial, we cleaned the enclosures to remove debris that built up on the mesh, especially on the upstream sides. Enclosures were cleaned three times weekly (Monday, Wednesday, Friday) in 2002. We increased cleaning frequency to 6 $days{\cdot}week^{-1}$ (Monday – Saturday) during 2003 and 2004 to increase water flow through the enclosures (Zimmerman and Vondracek 2006). While cleaning, we examined enclosures for dead fish. We assumed that fish found dead during the first 5 days of each experimental trial had died because of handling stress, thus we replaced these fish. Fish found dead after 5 days were not replaced. We measured water depth and water velocity at three random points in enclosures three times during each experimental trial, before and after removing debris.

Table 1. Design of experiments examining intra- and inter-specific competition between slimy sculpin (*Cottus cognatus*) and each trout species (brook, *Salvelinus fontinalis*; and brown, *Salmo trutta*) for trout-only, combined species, and sculpin-only treatments.

	No. of fish per treatment		
Density design	Trout only	Combined species	Sculpin only
Unequal additive			
Sculpin	—	3	3
Trout	1	1	—
Equal additive			
Sculpin	—	3	3
Trout	3	3	—
Substitutive			
Sculpin	—	2	4
Trout	4	2	—

Note: Density designs (refer to Materials and methods) were randomly assigned to riffles within blocks of stream reach, and fish species treatments were randomly assigned to enclosures within riffles (a split-plot design).

Statistical analyses

Recovery rates

We examined the recovery rates of each species at the end of each experimental trial as an estimate of survival. We used a logistic regression analysis, with the response variable equal to the number of each species recovered from each enclosure at the end of each experimental trial out of the number of each species placed in each enclosure at the beginning of each experimental trial. We eliminated experimental trials conducted during June 2002 and June 2003 from the analysis of recovery rates because high discharge events resulted in destruction of many enclosures on the final day of these trials. We analyzed a separate logistic regression model per species, with each model containing one blocking variable at the whole-plot level (experimental trial × stream reach, eight levels), one whole-plot factor (density, three levels), one split-plot factor (fish species treatment: two levels for trout and three levels for sculpin), and one covariate (mean initial mass of each species per enclosure). We included mean initial mass of each species as a covariate to examine if recovery rates varied with fish size.

Growth

We compared growth of each species in combined species treatments with growth of each species alone for all experimental trials using an analysis of covariance (ANCOVA), and data from all trials were included. Because each fish species treatment occurred in each riffle, we paired the sin-

Table 2. Dates of each experimental trial, mean initial mass of each fish species (±1 standard error) used, and percentage of slimy sculpin (*Cottus cognatus*), brook trout (*Salvelinus fontinalis*), and brown trout (*Salmo trutta*) recovered at the end of each trial.

Experimental trial date		Mean initial mass (g)			% Recovered*		
Start	End	Sculpin	Brook	Brown	Sculpin	Brook	Brown
13 May 2002	22 June 2002	5.5 (0.3)	13.5 (1.1)	14.3 (1.0)	76	50	75
25 June 2002	4 August 2002	19.0 (0.9)	38.2 (2.2)	75.0 (2.5)	83	72	44
5 August 2002	12 September 2002	11.3 (0.5)	11.4 (0.9)	12.8 (0.5)	76	92	83
19 May 2003	25 June 2003	6.3 (0.3)	24.8 (0.9)	26.5 (1.0)	66	2	24
21 July 2003	27 August 2003	6.4 (0.3)	6.8 (0.3)	8.2 (0.2)	92	95	93
14 July 2004	20 August 2004	7.3 (0.3)	4.3 (0.2)	6.9 (0.2)	96	76	100

*Fish not recovered may have escaped from enclosures or died during the experiment. High stream flows destroyed many enclosures during experiments ending in June 2002 and June 2003.

gle species control with the combined species treatment for each riffle and analyzed the difference in growth between each paired treatment and control. Therefore, for this analysis, riffle was our experimental unit for both factors of interest (fish species treatment and density design). Our response variable was growth of each species in combined species treatments minus growth of each species alone. We analyzed four ANCOVA models: (*i*) growth of brook trout with sculpin minus growth of brook trout alone; (*ii*) growth of brown trout with sculpin minus growth of brown trout alone; (*iii*) growth of sculpin with brook trout minus growth of sculpin alone; and (*iv*) growth of sculpin with brown trout minus growth of sculpin alone. Our models included one blocking variable (experimental trial × reach, 12 levels), one factor (density, three levels), and two covariates (difference in initial fish mass between treatment and control and mean initial fish mass).

For the growth analysis, significance levels ($\alpha = 0.05$) of independent variables represented the degree to which each variable interacted with effects of fish species treatment. Responses that were different from zero represented a significant difference in growth between treatment and control. We examined responses for each density design and significant covariates using the Tukey–Kramer multiple comparison test for unequal cell sizes (SAS Institute Inc. 1999). Of the total 45 possible comparisons between treatment and control (three trials using six riffles plus three trials using nine riffles), we used data for 28 brook trout comparisons, 29 brown trout comparisons, 38 comparisons of sculpin alone to sculpin with brook trout, and 36 comparisons of sculpin alone to sculpin with brown trout. We could not use all 45 comparisons for each analysis because of the number of enclosures lost during high flow events (i.e., fish were not recovered from all enclosures).

Results

Recovery rates

Recovery rates of individual fish during each experimental trial were generally >75%, except for experiments ending in June 2002 and 2003 (Table 2). We rarely observed dead fish in enclosures, even though we examined enclosures between 3 and 6 days per week during cleaning. Therefore, we could not determine whether losses of fish (unrelated to the loss of entire enclosures) were due to mortality or escapement. The majority of unexplained fish losses during 2002 occurred in two riffles located in a reach with smaller substrate, more riparian vegetation, and more shading than the rest of our study area (proportion of total losses = 46% of brook trout, 58% of brown trout, and 76% of sculpin for experimental trials ending in August and September 2002). Therefore, we did not use those riffles for our experimental trials during 2003 and 2004; instead, we chose riffles with characteristics more comparable with the other riffles.

Recovery of the two trout species was not associated with presence or absence of sculpin (Fig. 1). Brook trout recovery rates varied among experimental trials and stream reaches, although the overall effect of experimental trial × reach was not significant ($p = 0.14$). Variation in brook trout recovery was not explained by density ($p = 0.56$), fish species treatment ($p = 0.08$), or initial mass of brook trout ($p = 0.19$). Brown trout recovery was not significantly influenced by experimental trial × reach ($p = 0.72$), density ($p = 0.75$), or fish species treatment ($p = 0.23$), but recovery of brown trout significantly decreased as initial mass of brown trout increased ($p = 0.01$; the proportion of fish recovered decreased by 19% with each 1 g increase in fish mass; 95% confidence interval = 6%, 31%). The logistic regression analysis explained 28% of variation in brook trout recovery (likelihood ratio test $p = 0.01$; correct classification rate = 81%) and 52% of variation in brown trout recovery (likelihood ratio test $p < 0.01$; correct classification rate = 90%).

Sculpin had significantly lower recovery rates when they were with brown trout compared with when they were alone ($p = 0.04$; Fig. 1); sculpin recovery decreased by 63% (95% confidence interval = 9%, 86%) when they were with brown trout. There was no significant difference in recovery of sculpin when they were alone compared with treatments with brook trout ($p = 0.88$; Fig. 1). Recovery of sculpin was not significantly explained by experimental trial × reach ($p = 0.44$), density ($p = 0.21$), or initial sculpin mass ($p = 0.18$). The logistic regression analysis explained 25% of variation in sculpin recovery (likelihood ratio test $p < 0.01$; correct classification rate = 81%).

Growth

Growth of brook trout with sculpin was not significantly different from growth of brook trout alone, regardless of density and initial brook trout mass (Fig. 2). Neither the overall ANCOVA model (ANCOVA: $F = 1.75$; df = 13, 15; $p = 0.15$; $R^2 = 0.58$) nor any parameters were significant ($p = 0.92$ for experimental trial × reach; $p = 0.85$ for density;

Fig. 1. Mean observed proportions of fish recovered (survival; ±2 standard errors) of (*a*) brook trout (*Salvelinus fontinalis*, solid bars) and brown trout (*Salmo trutta*, open bars) and (*b*) slimy sculpin (*Cottus cognatus*) among fish species treatments for all experimental trials. Logistic regression models indicated that trout survival was not significantly ($\alpha = 0.05$) different between treatments, whereas sculpin survival was lower in treatments with brown trout than in treatments alone or with brook trout.

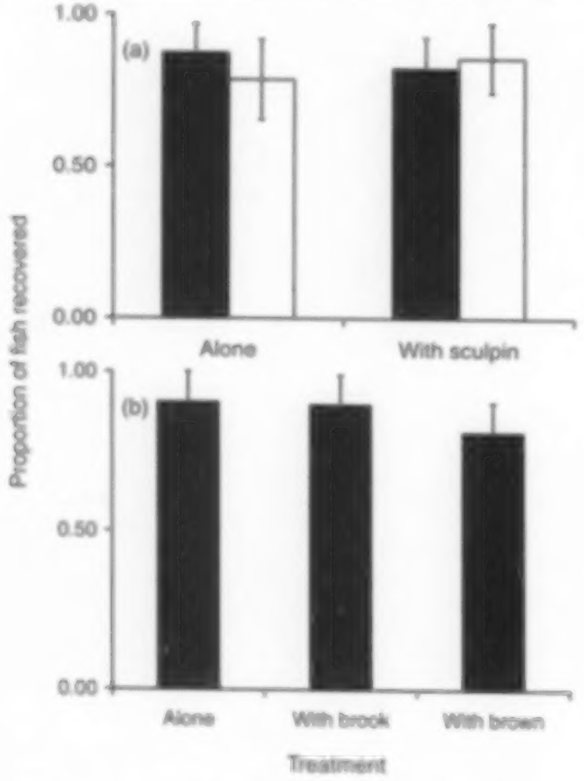


Fig. 2. Difference in change in mass (growth; ±2 standard errors) for brook trout (*Salvelinus fontinalis*) between fish species treatments (growth of brook trout with slimy sculpin, *Cottus cognatus*, minus growth of brook trout alone). Brook trout initial mass represents minimum, mean, and maximum mass across all six experiments. Density designs are represented as follows: unequal additive, open bars; equal additive, shaded bars; substitutive, solid bars.

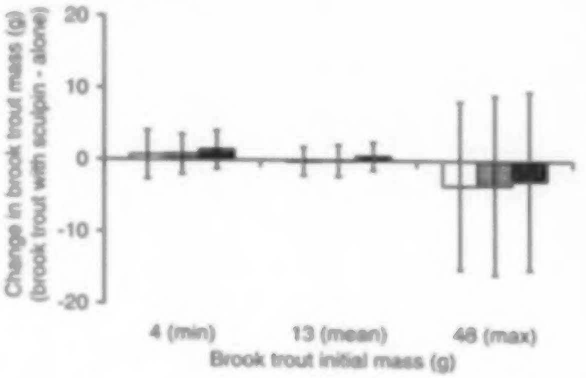
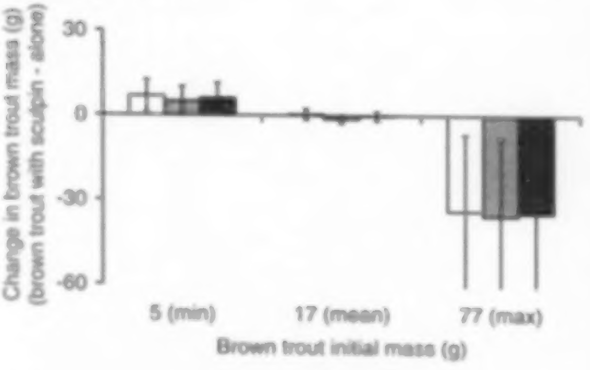


Fig. 3. Difference in change in mass (growth; ±2 standard errors) for brown trout (*Salmo trutta*) between fish species treatments (growth of brown trout with slimy sculpin, *Cottus cognatus*, minus growth of brown trout alone). Brown trout initial mass represents minimum, mean, and maximum mass across all six experiments. Density designs are represented as follows: unequal additive, open bars; equal additive, shaded bars; substitutive, solid bars.



$p = 0.57$ for mean initial mass; and $p = 0.08$ for difference in initial mass between each treatment–control pair).

Brown trout growth with sculpin tended to be different than growth of brown trout alone, depending on initial mass of brown trout ($p = 0.02$ for overall effect of mean initial mass). Tukey–Kramer multiple comparison tests indicated that the smallest brown trout used in our experiments (5.4 g) grew significantly more with sculpin than alone regardless of density design (Fig. 3), with a difference in growth between treatments of approximately 6 g. At the mean size of brown trout used in all our experiments (17 g), there was no effect of fish species treatment on growth. However, larger brown trout (≥25 g) grew significantly faster when alone than with sculpin (Fig. 3). Small brown trout (<5.5 g) comprised 4% and large brown trout (≥25 g) comprised 15% of the total brown trout used in our analysis. At the largest brown trout size used in our experiment (77 g), the estimated mean difference in growth between treatment and control was 34 g. The influence of brown trout mass on fish species treatment effects was the same for all densities; thus a change in mass was equivalent whether brown trout were replaced by sculpin (substitutive design) or sculpin were added to a constant number of trout (additive designs). Overall, the model we used to examine growth of brown trout explained 70% of the variation in the difference in growth between pairs of treatment and control enclosures (ANCOVA; $F = 2.67$; df = 14, 15; $p = 0.03$; $R^2 = 0.70$). Experimental trial and stream reach ($p = 0.62$), density ($p = 0.40$), and difference in initial brown trout mass between each treatment–control pair ($p = 0.06$) did not explain significant variation in growth.

Sculpin growth with brook trout was not significantly different from growth of sculpin alone, regardless of density or either covariate, indicating no evidence of an interaction between sculpin and brook trout (Fig. 4*a*). Neither the overall ANCOVA model ($F = 0.42$; df = 16, 22; $p = 0.96$; $R^2 =$

0.22) nor any parameters in the model were significant (p = 0.89 for experimental trial × reach; $p = 0.79$ for density; p = 0.85 for difference in initial sculpin mass between treatment and control; $p = 0.56$ for mean initial mass of sculpin).

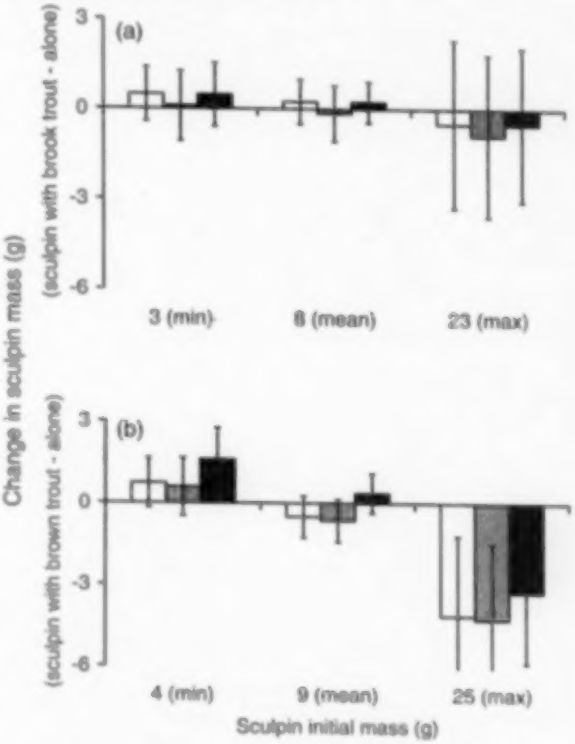
Sculpin growth with brown trout was significantly different from growth of sculpin alone when sculpin were large ($p = 0.01$ for overall effect of mean initial mass). Tukey–Kramer multiple comparison tests indicated that large sculpin (>16 g) grew significantly less in treatments with brown trout than when they were alone (Fig. 4*b*). Large sculpin (>16 g) comprised 11% of the total number of sculpin used in our analysis. At the largest sculpin sizes (24 g), the mean difference in growth between treatment and control was 4 g. The effects of sculpin mass and presence of brown trout on growth were the same when sculpin were replaced by an equal number of brown trout (substitutive design) as when brown trout were added to a constant density of sculpin (additive designs). Small (4 g) and mean-sized (9 g) sculpin showed no difference in growth when they were with brown trout versus alone. The overall ANCOVA model explained 47% of variation in sculpin growth when they were alone versus with brown trout ($F = 1.16$; df = 16, 20; $p = 0.37$; $R^2 = 0.47$). Experimental trial × reach ($p = 0.85$), density ($p = 0.16$), and difference in initial mass between each paired treatment and control ($p = 0.36$) did not explain a significant amount of variation in growth.

Discussion

Introductions of brown trout and other gamefish species have altered fish communities throughout the United States, contributing to homogenization of fish faunas (Rahel 2000, 2002; Olden et al. 2004). The most visible effects of species introductions include major changes in range or abundance and, in many instances, extirpation of native fish (Cambray 2003). However, less obvious consequences include increased competition for food, space, or other resources with native species that may result in changes in growth or fitness. In our experiment, we found no evidence of competition between two native species (brook trout and slimy sculpin), measured by recovery rates or changes in growth. In contrast, brown trout and sculpin interacted more strongly, potentially because of interference between individuals. Growth of large sculpin was reduced when nonnative brown trout were present. Slimy sculpin may have facilitated growth of brown trout when trout were small, but growth of brown trout was reduced in the presence of sculpin as trout size increased. Slimy sculpin had no effect on recovery rates of brown trout; however, presence of brown trout was associated with decreased recovery rates of sculpin. The combination of decreased sculpin growth and recovery suggests the potential for strong effects of nonnative brown trout on sculpin populations.

Brook trout and slimy sculpin are morphologically dissimilar species but often occur together in their native range; thus, we predicted that juveniles of these species may have developed different foraging strategies and would not compete. Although brook trout and slimy sculpin feed on similar prey items in Valley Creek, brook trout primarily consume drifting prey during daylight hours, whereas sculpin are benthic feeders and often feed at night (Petrosky and Waters 1975). There is limited evidence of predation between different life stages of brook trout and sculpin. Slimy sculpin have been shown to avoid brook trout large enough to pose a predation threat, although they did not avoid small brook trout (Chivers et al. 2001). Although we did not find evidence of competition between juvenile brook trout and slimy sculpin, large brook trout may prey on smaller sculpin.

Fig. 4. Difference in change in mass (growth; ±2 standard errors) for slimy sculpin (*Cottus cognatus*) between (*a*) sculpin with brook trout (*Salvelinus fontinalis*) and sculpin alone and between (*b*) sculpin with brown trout (*Salmo trutta*) and sculpin alone. Sculpin initial mass represents minimum, mean, and maximum mass across all six experiments. Density designs are represented as follows: unequal additive, open bars; equal additive, shaded bars; substitutive, solid bars.



Brown trout and slimy sculpin are also morphologically dissimilar species; however, they do not occur together in their native ranges and brown trout may be competitively superior to slimy sculpin (Ruetz et al. 2003). Brown trout were shown to reduce sculpin growth in another enclosure experiment conducted in Valley Creek, potentially by feeding on and reducing benthic prey populations (Ruetz et al. 2003). An enclosure experiment conducted in a Swedish stream found that bullhead (*Cottus gobio*) fed heavily on the benthos, reducing densities of seven invertebrate taxa, whereas brown trout had a much weaker effect on benthic prey (Dahl 1998). However, more than 80% of the diet of brown trout in Dahl's (1998) study consisted of terrestrial invertebrates, and drift-feeding salmonids have been shown to feed on benthic invertebrates when terrestrial prey are not available (Nakano et al. 1999*a*, 1999*b*; Baxter et al. 2004). In a study of brown trout diets in Valley Creek, terrestrial invertebrates made up only 3.1% of the total biomass of prey ingested (Laudon et al. 2005). Thus, a lack of terrestrial prey may cause brown trout to shift to benthic feeding. In addition, brown trout have been shown to forage nocturnally (Alanara et al. 2001). Overlap in foraging strategies, such as benthic feeding and lack of temporal segregation in foraging activity, was a potential mechanism underlying competitive interactions between sculpin and brown trout. Brown trout may also have displaced sculpin from resting locations, thus increasing activity costs. Light (2005) found that nonnative signal crayfish (*Pacifastacus leniusculus*) increased activity rate and reduced growth of native Paiute sculpin (*Cottus beldingii*) by displacing the sculpin from refuges and pools into higher velocity habitats.

In addition to similar foraging strategies between sculpin and brown trout, adult trout pose a threat of predation for small- to medium-sized sculpin (Garman and Nielsen 1982; Chivers et al. 2001). Suppression of sculpin growth at small sizes may make sculpin susceptible to trout predation for longer periods of time. A similar effect was seen in interactions between native masu salmon (i.e., cherry salmon, *Oncorhynchus masou masou*) and nonnative rainbow trout in a Japanese stream, where competition between species reduced masu salmon growth and may have increased the vulnerability of small masu salmon to predation by age-1 rainbow trout (Taniguchi et al. 2002). Mills et al. (2004) found that competition between native least chub (*Lotichthys phlegethontis*) and nonnative western mosquitofish (*Gambusia affinis*) decreased growth of least chub, increasing the vulnerability of juveniles to mosquitofish predation.

Although we predicted that brown trout would reduce sculpin growth, we did not expect to see evidence of sculpin reducing growth of large brown trout. Another enclosure experiment conducted in Valley Creek did not find changes in brown trout growth when sculpin were present, although the brown trout used in that experiment were all age-0 (Ruetz et al. 2003), thus comparable only with small brown trout used in our study. Other recent studies have suggested that brown trout and sculpin may compete over prey items and preferred habitat, with sculpin often being competitively superior. Hesthagen et al. (2004) found an inverse relationship between densities of juvenile brown trout and Siberian sculpin (i.e., alpine bullhead, *Cottus poecilopus*) in a Norwegian river within the native range of both species. The authors suggested that this relationship, coupled with high diet overlap between the species, indicated a potential for competitive interactions. Hesthagen and Heggenes (2003) conducted experiments in artificial stream channels and found that Siberian sculpin displaced young brown trout from preferred habitats, whereas habitat selection of large Siberian sculpin did not change regardless of brown trout presence.

Contrary to our predictions, we also observed evidence of facilitation between sculpin and young brown trout, because small brown trout growth increased in treatments with sculpin. Predator facilitation may occur when predation strategies of one species increase the vulnerability of prey to another species that forages differently (Matsuda et al. 1993; Soluk and Richardson 1997). Ruetz et al. (2003) predicted predator facilitation between brown trout and sculpin in an enclosure experiment because benthic feeding by sculpin may increase invertebrate drift (Miyasaka and Nakano 1999), thus increasing availability of invertebrate prey for drift-feeding brown trout. However, Ruetz et al. (2003) did not observe predator facilitation in their experiment. We may have had a greater opportunity to investigate the potential for predator facilitation and interspecific competition in our experiments because of the greater amount of spatial and temporal replication and the broader range of fish sizes and densities in our study.

In a concurrent study, Zimmerman and Vondracek (2006) examined potential effects of the 1 m^2 stream enclosures used in these experiments on fish growth, rates of water flow, and invertebrate drift. In single species treatments, growth of brook and brown trout was affected by the interaction of fish size and density. Growth of both trout species generally decreased as biomass of trout within an enclosure increased. However, slimy sculpin growth was not influenced by fish size or density. Growth of brook trout, brown trout, and sculpin was not limited by low prey availability (measured by invertebrate drift rate). Although enclosures tended to restrict water flow and decrease drift rate, drift density was similar behind enclosures compared with adjacent riffle areas; thus the enclosures did not have a large effect on availability of drifting invertebrate prey.

Zimmerman and Vondracek's (2006) study provided evidence of intraspecific competition for both trout species at high fish biomass within the enclosures. We would only expect to observe interspecific competition under conditions where intraspecific competition also occurs, because individuals within a species have more similar resource requirements than individuals of different species (Underwood 1986). Therefore, we would expect competitive interactions to increase with size for both species of trout because resources within the enclosures are likely limited for large trout sizes. We observed evidence of interspecific competition for interactions between brown trout and sculpin, but not for interactions between brook trout and sculpin. This suggests that growth of juvenile brook trout is more influenced by intraspecific competition than by interactions with sculpin, whereas brown trout show evidence of interspecific competition with sculpin when resources are potentially limiting.

Sculpin biomass was not high enough in enclosures to observe evidence of intraspecific competition when sculpin were alone (Zimmerman and Vondracek 2006); however, the addition of brown trout to enclosures, as well as the substitution of half the sculpin with an equal number of brown trout, resulted in a decrease in sculpin growth. Potentially, resource use by brown trout was greater than that of sculpin, and sculpin were less able to compete with brown trout when resources were limiting (when sculpin size was large). We may not have observed differences in fish species treatment effects among density designs (unequal additive, equal additive, and substitutive) because the differences in relative species densities between our density designs may not have been large enough to detect differences in these interactions. However, it is likely that the changes in sculpin growth that we observed resulted from changes in sculpin behavior according to presence or absence of brown trout (regardless of brown trout density), rather than resource limitation. In another concurrent study, Zimmerman (2005) found a shift in sculpin diet when brown trout were present in enclosures, regardless of sculpin size, relative density of each species, or total fish density. In contrast, there was no evidence of a shift in sculpin diet when brook trout were present. If the presence of brown trout caused sculpin to change their feeding behavior, this may have been reflected in diet and ultimate reductions in growth.

Although the presence of brown trout was associated with reduced recovery of sculpin and growth of large sculpin in our experiments, we do not expect this apparent competition to result in extirpations of sculpin from Valley Creek. Brown trout and sculpin have coexisted in Valley Creek for over 100 years, and sculpin are the most abundant (numerically) fish species in the stream (Petrosky and Waters 1975; Ruetz et al. 2002). Mårschall and Crowder (1996) examined effects of introduced rainbow trout on brook trout growth and survival and modeled a potential response of the brook trout population. Survival of juveniles was density dependent, and fish reproduced at small sizes. Therefore, decreased survival of small juveniles and large fish, as well as growth of large fish, did not lead to large changes in the brook trout population. Valley Creek has high invertebrate productivity (Waters and Hokenstrom 1980), and fish abundance may be regulated by space and shelter requirements rather than by prey availability (Petrosky and Waters 1975; Zimmerman and Vondracek 2006). If survival of juvenile sculpin depends on availability of space and shelter, presence of brown trout may lead to reductions in juvenile abundance, but not long-term population declines of sculpin in Valley Creek. Our study examined species interactions over multiple years using different densities and sizes of fish; thus, variation in prey availability and environmental conditions were incorporated into our experimental design. Therefore, we believe that our study is applicable to other streams with high prey availability and relatively stable temperature and hydrologic conditions. However, we predict that brown trout may have a stronger effect on sculpin populations in streams where prey is limited or environmental conditions are more variable.

It is possible that presence of nonnative rainbow trout may also decrease sculpin growth in Valley Creek, although we did not include rainbow trout in our study because they had low abundance relative to brown trout (Waters 1999). A study of habitat use by nonnative rainbow trout and Little Colorado spinedace (*Lepidomeda vittata*, a native nongame fish) found few agonistic interactions between the species, although spinedace may shift habitat use at high densities of rainbow trout (Robinson et al. 2003). Additional experiments that examine sculpin population dynamics with native and nonnative trout are needed to determine potential effects of multiple trout introductions on sculpin abundance.

Overall, we found that brown trout and brook trout interact differently with slimy sculpin, thus providing evidence that native and nonnative trout do not fill the same ecological role in stream communities, and replacement of a native trout by a nonnative trout can result in changes to growth and survival of native nongame fish. Baxter et al. (2004) found that nonnative rainbow trout caused native Dolly Varden (*Salvelinus malma*) to shift their foraging behavior, resulting in changes to stream and riparian ecosystems. Similarly, we found that a native and a nonnative trout, though similar ecologically, can have very different effects on stream communities. Our results also suggest that the two native species may have evolved to fill different ecological niches in stream riffles, resulting in minimal interspecific competition. In contrast, brown trout and sculpin exhibited interspecific interactions that resulted in decreased growth of both species when individuals were large, and growth continued to decrease as size of each species increased. Further research is needed to address potential mechanisms underlying these interactions between brown trout and sculpin, including changes in feeding strategies, feeding positions within enclosures (sensu Fausch and White 1981), or behavior, when both species are together relative to each species alone. Interactions between nonnative sportfish and native nongame fish and potential effects on freshwater biodiversity are growing concerns for fisheries biologists and managers (Clarkson et al. 2005). Our investigation of ecological differences between native and nonnative trout and relative effects on a nongame fish will help to inform management of native fish and assess potential risks of introduced trout in aquatic ecosystems.

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Mapping seabed assemblages using comparative top-down and bottom-up classification approaches

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Abstract: Acoustic technologies yield many benefits for mapping the physical structure of seabed environments but are not ideally suited to classifying associated biological assemblages. We tested this assumption using benthic infauna data collected off the south coast of England by applying top-down (supervised) and bottom-up (unsupervised) classification approaches. The top-down approach was based on an a priori acoustic classification of the seabed followed by characterization of the acoustic regions using ground-truth biological samples. By contrast, measures of similarity between the ground-truth infaunal community data formed the basis of the bottom-up approach to assemblage classification. For both approaches, individual assemblages were mapped by first computing Bayesian conditional probabilities for ground-truth stations to estimate the probability of each station belonging to an assemblage. Assemblage distributions were then interpolated over a regular grid and characterized using an indicator value index. While the two methods of classification yielded assemblages and output maps that were broadly comparable, the bottom-up approach arrived at a slightly better defined set of biological assemblages. This suggests that acoustically derived seabed data are not ideally suited to classifying biological assemblages over unconsolidated sediments, despite offering considerable advantages in providing rapid and low-cost assessments of seabed physical structure.

Résumé : Les technologies acoustiques sont très utiles pour faire la cartographie de la structure physique des environnements des fonds marins, mais ce ne sont pas des méthodes idéales pour classifier les peuplements biologiques associés. Nous testons cette présupposition à l'aide de données sur l'endofaune benthique récoltées au large de la côte méridionale de l'Angleterre en leur appliquant des méthodes de classification descendantes (supervisées) et ascendantes (non supervisées). La méthode descendante est basée sur une classification acoustique a priori du fond marin suivie d'une caractérisation des régions acoustiques à l'aide d'échantillons biologiques réels récoltés sur place. En revanche, les mesures de similarité entre les données réelles de la communauté endofaunique servent de base à la méthode ascendante de classification des peuplements. Dans les deux méthodes, la cartographie des peuplements individuels implique d'abord le calcul des probabilités bayésiennes conditionnelles pour les stations réelles afin d'estimer la probabilité de chaque station d'appartenir à un peuplement. Nous interpolons ensuite la répartition des peuplements sur une grille régulière et les caractérisons à l'aide d'un indice de valeur indicatrice. Bien que les deux méthodes de classification produisent des peuplements et des cartes de distribution qui sont en gros comparables, la méthode ascendante fournit un ensemble de peuplements biologiques définis avec plus de précision. Ces résultats indiquent que des données acoustiques sur les fonds marins ne sont totalement appropriées pour faire une classification des peuplements biologiques sur des sédiments non consolidés, même si elles présentent des avantages considérables pour une évaluation rapide et peu coûteuse de la structure physique des fonds marins.

[Traduit par la Rédaction]

Introduction

Marine acoustic technologies have changed the way seabed environments and the biological assemblages they support are classified and mapped. Acoustic systems are able to acquire 100% coverage data on seabed geology and geomorphology over relatively broad spatial scales, offering an unprecedented level of resolution, coverage, and spatial

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definition to modern-day seabed maps (Kenny et al. 2003). The most commonly applied method of mapping seabed environments using acoustic technologies is to acoustically survey an area of seabed, define boundaries between different seabed structures, and then identify biological features and assemblages within each region via ground-truth, point-source sampling. Seabed mapping based on this approach has been undertaken using all three principal marine acoustic technologies: sidescan sonar (e.g., Brown et al. 2002, 2004), acoustic ground discrimination systems based on normal incidence single-beam echo sounders (e.g., Greenstreet et al. 1997; Kloser et al. 2001; Foster-Smith et al. 2004), and multibeam echo sounders (e.g., Kostylev et al. 2001; Roberts et al. 2005). As acoustic data are less able to detect changes in the biological components of the seabed, classifications of different seabed environments tend to be driven largely by physical criteria. This top-down or supervised approach to mapping biological assemblages imposes a physically based classification scheme that may not be ideal and may lead to a range of biological assemblages being found within a single physical habitat (Zajac et al. 2000; Brown et al. 2002) or similar assemblages being found in more than one physical habitat (Kostylev et al. 2001; Freitas et al. 2003). There is no doubt that acoustic technologies have greatly improved maps of the physical aspects of seabed environments and provided unique insights in biological community structure and distribution. In areas of seabed characterized by a high degree of sediment heterogeneity, our understanding of community structure and the spatial distributions of biological assemblages is strengthened through the combined use of acoustic data and point-source biological samples. When surveying large areas of seabed, biological sampling at high intensity is unlikely to be cost-effective, and if acoustic data are not collected alongside, small-scale patchiness in the seabed environment will likely be missed. Given the benefits of acoustic systems to seabed mapping, it is not surprising that acoustically derived data would be used as the primary basis by which to classify seabed environments in terms of both physical and biological components.

In the absence of acoustic data, the alternative to classifying biological assemblages is to allow associations to form between point-source biological community samples based on measures of similarity, such as Bray–Curtis. This type of approach to classifying biological assemblages can be thought of as bottom-up or unsupervised, as no external structure is imposed. Once a suitable classification has been generated, maps of biological assemblages are typically generated by symbolizing the point locations accordingly (e.g., Jennings et al. 1999; Kaiser et al. 1999; Stevens and Connolly 2004). The exact positioning of spatially discrete boundaries between assemblages can then be estimated subjectively (Rees et al. 1999). A more objective approach to estimating the spatial distribution of individual assemblages would be to interpolate point-source univariate metrics or estimate patterns of distribution at unsampled locations using proxies in a way similar to that used for single-species distribution modelling (e.g., Boyce and McDonald 1999; Guisan and Zimmerman 2000; Eastwood and Meaden 2004). Unfortunately standard assemblage classification techniques do not arrive at measures that can be mapped using these approaches. A further problem is that while biological assemblages associated with spatially discrete features such as seagrass beds and reefs may be suited to mapping with hard physical boundaries, assemblages associated with unconsolidated sediments tend to show a more gradual development from one assemblage to the next. A number of methods capable of describing assemblages as continua have recently been explored (Souissi et al. 2001; Caeiro et al. 2003; ter Braak et al. 2003). In environments where more gradual changes would be expected, there may be little advantage to the use of top-down approaches if the main purpose of the mapping exercise is to better understand the spatial distribution of the benthic community. Bottom-up or unsupervised approaches to biological assemblage classification may instead be better able to detect differences between individual assemblages (Hewitt et al. 2004); combined with multivariate mapping techniques, bottom-up approaches can also lead to maps where the biological assemblages are described as continua and thus with improved spatial accuracy.

To assess biological assemblage classifications based on top-down and bottom-up approaches and to compare output maps, we applied the multivariate mapping method of Souissi et al. (2001) in supervised and unsupervised mode to benthic infauna data collected from an area of gravels and sands, i.e., unconsolidated sediments. A top-down approach to seabed mapping at this site has already been presented by Brown et al. (2002), where it was found that the acoustically classified regions in some cases appeared to contain more than one assemblage. Our primary objective was to assess whether a bottom-up approach would arrive at a more distinct and better-defined set of assemblages compared with a top-down classification if the primary focus is on obtaining a map of biological assemblages and not biotopes per se, i.e., combined physical and biological classification.

Materials and methods

Acoustic survey

The study area is located off the south coast of England and has been previously described by Brown et al. (2002) (Fig. 1). An intensive acoustic survey of the entire area was conducted in July 1999 using digital sidescan sonar. Postprocessing software was used to mosaic the imagery. The system was operated on a 400 m swathe range, and survey lines were spaced at 400 m intervals in a north–south orientation to ensonify 100% of the survey area. Vessel position was provided by differential global positioning system, and towed sensor position was calculated from estimates of vessel heading, tow cable layback, and towfish depth, all of which were logged in real time. A drop-camera frame fitted with an underwater video camera and light was deployed at a number of stations across the survey area to provide visual ground-truth data to aid interpretation of the sidescan sonar data set. Following the cruise, the sidescan mosaic was used to classify the survey area into eight acoustically distinct regions based on a visual interpretation of the imagery (labelled A, B, C, D, E, F, H, and H/F in Fig. 1). Further details of the sidescan survey are given in Brown et al. (2002).

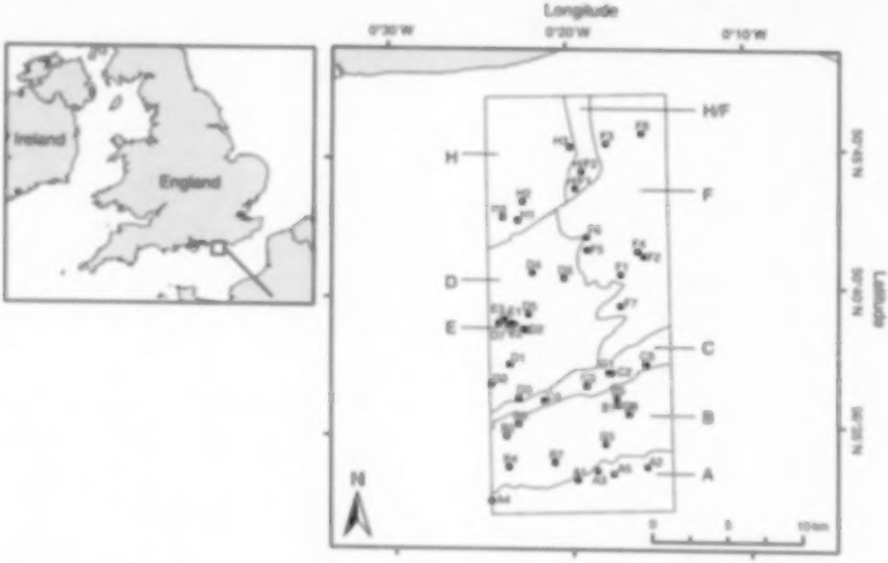


Fig. 1. Location of the study site and plan of the surveyed area showing the eight acoustically classified regions and Hamon grab sample stations (solid squares).

Benthic survey

The design of the macrobenthic grab survey was structured around the eight regions identified from the acoustic survey. Sampling stations were randomly positioned within each acoustic region, with the number of stations within each region proportional to its size. The survey was conducted in August 1999 with a total of 43 samples collected from across the survey area using a 0.1 m^2 Hamon grab. Following estimation of the total grab sample volume, a 500 mL subsample was removed for laboratory particle size analysis. The remaining sample was washed over a 1 mm^2 mesh sieve to remove excess sediment. Specimens were identified to species level, or as far as possible, using standard taxonomic keys. The number of each species was recorded, and colonial species were recorded as present or absent. Further details of the benthic survey are given in Brown et al. (2002).

Assemblage mapping — unsupervised classification

The approach used to map the biological assemblages was based on a modified version of the method of Souissi et al. (2001) as described in Anneville et al. (2002). A summary of the method is given below.

Selection of taxa and classification of assemblages

Only burrowing and infaunal species were used in the analysis; epifaunal species are not sampled efficiently by Hamon grabs. This group contained 155 taxa and most were of low abundance, so only the 40 most abundant taxa were retained for further analysis. This number of taxa was chosen arbitrarily but represented a sensible trade-off in retaining sufficient taxa for the analysis while at the same time reducing the number of rare or low-occurrence species (the 40 selected taxa were present in at least 6 of the 43 stations, i.e., 12%). A principal component analysis (PCA) was then performed on double-root-transformed species counts. Transformation of the species counts into PCA scores was necessary to ensure multinormality in the data, a requirement for computing Bayesian probabilities at the next stage of the analysis (see below). PCA scores from the first 25 axes, which explained over 97% of the total variance in the species data, were then subject to a hierarchical classification based on Euclidean distance with flexible links clustering (Legendre and Legendre 1998). This produced a dendrogram from which station groups (clusters) could be defined at selected cutoff levels. Station groups were considered to represent biological assemblages.

Computation of conditional probabilities

Once an appropriate cutoff level had been decided, Bayesian conditional probabilities were calculated to represent the probability of each station belonging to a station group (Harff and Davis 1990; Harff et al. 1993). Depending on the PCA scores assigned to each station O_i, the probability that it belonged to a station group G_j is given by

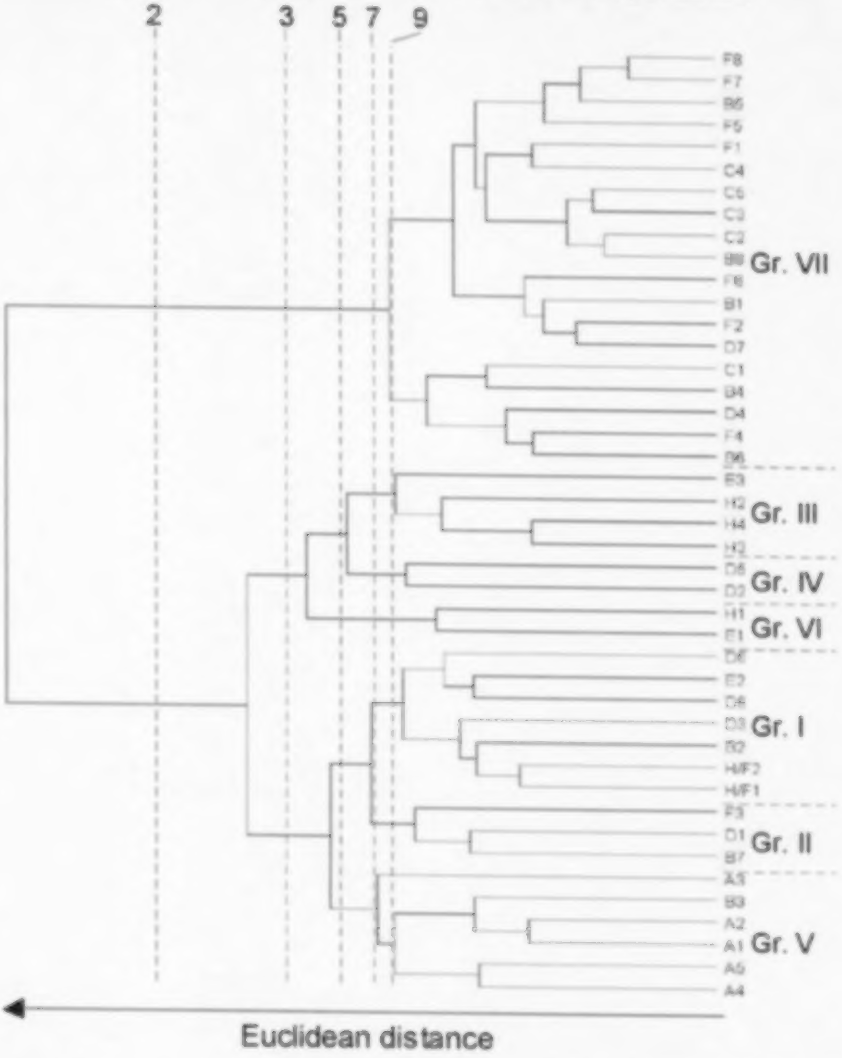
$$(1)\qquad P(O_i \in G_j) = \frac{p_j \left| \sum_j \right|^{-1/2} \exp\left[-d_j^2(i)/2\right]}{\sum_{k=1}^{g} p_k \left| \sum_k \right|^{-1/2} \exp\left[-d_k^2(i)/2\right]}$$

Here, p_j is an a priori probability representing the proportion of stations in the station group G_j to the total number of stations (43), and $d_j^2(i)$ is the generalized Mahalanobis distance between G_j and O_i:

$$(2)\qquad d_j^2(i) = (O_i - m_j^G)^t \sum_j^{-1} (O_i - m_j^G)$$

where m_j^G is the centroid of the station group G_j, i.e., the mean of the scores for the principal axes in the dimension of samples. A pooled variance–covariance matrix was used as a

Fig. 2. Dendrogram of Hamon grab stations based on levels of similarity (Euclidean distance, flexible links clustering, between principal component analysis (PCA) scores). Cutoff levels for two, three, five, seven, and nine station groups are shown by the vertical broken lines. Stations partitioned by the seven station group cutoff level are indicated on the right-hand side.



substitute for the normal dispersion matrix when computing d^2.

Assemblage mapping

Deciding on an appropriate cutoff level for the dendrogram needed some consideration, as a slight shift to a higher or lower degree of similarity could potentially have a marked effect on the final number of mapped assemblages. First, we took the decision that a partition of stations into more than eight groups was unlikely to produce a set of assemblages that were substantially different from each other, given that the study area covered a relatively small geographic region and the seabed consisted of fairly uniform, mobile sands and gravels (Brown et al. 2002). At each hierarchical level from 2 to 8, we next computed the maximum conditional probability for each station. Maximum probabilities were most often associated with the group to which the station had been allocated, but in a small number of cases (<1%) the maximum probability for a station was given through its association to a different group. At each hierarchical level k, the median probability $P_m(k)$ of the maximum probabilities was then computed:

$$(3) \qquad P_m(k) = \text{median } P_{\max}(k)$$

This provided an average measure of the within-group homogeneity for each hierarchical level and could be used to determine an appropriate dendrogram cutoff level, i.e., where $P_m(k)$ was highest.

Conditional probabilities may be treated as regionalized variables (Harff et al. 1993), thus allowing the use of geostatistics and kriging interpolators to estimate conditional probabilities at unsampled locations, i.e., between stations.

Once a dendrogram cutoff had been decided and station groups defined, conditional probabilities associated with each station group were interpolated onto a regular grid of 10 000 m^2 (1 ha) cell size. The most appropriate theoretical variogram model was chosen to define the form of the kriging interpolator. The final set of maps provided estimates of the probability of a station belonging to a particular station group at each grid cell throughout the study area. A single assemblage map was produced by returning the station group associated with the highest probability at each grid cell. The map therefore depicted the assemblage most likely to occur at any given grid cell location.

Assemblage characterization

Species that characterized each assemblage were identified using the indicator value index of Dufrêne and Legendre (1997). The index combines measures of specificity and fidelity for a species within a station group relative to all other groups. Specificity reaches a maximum when species *i* is present in one group only, and fidelity reaches a maximum when species *i* is present in all stations within a station group. The indicator value index (IV) is the product of species fidelity (*F*) and specificity (*S*) and is represented as a percentage:

$$(4) \qquad \mathrm{IV} = (S{\cdot}F) \times 100$$

IV reaches a maximum (100%) when the individuals of species *i* are observed in all sites of only one station group. Species were retained as indicators of the station group if their associated IV was greater than 25% and maximum over all groups (Dufrêne and Legendre 1997; Souissi et al. 2001; Anneville et al. 2002).

Assemblage mapping — supervised classification

The classification and mapping procedure outlined above was repeated but this time with conditional probabilities computed for stations assigned to their respective acoustically distinct groups (see Fig. 1). Here, conditional probabilities represented the probability of each station belonging to the station groups as defined by the acoustic regions.

Results

Hierarchical classification of the PCA scores from the first 25 axes resulted in a dendrogram with relatively distinct station groups (Fig. 2). The first partition divided the stations into two major groups. Stations in one of the groups (marked Group VII in the dendrogram) were spatially contiguous and spanned the length of the survey area in a northeast to southwest orientation. The spatial definition of the other group was less clear, indicating that it consisted of a number of spatially distinct groups. Group VII remained a distinct group until it was finally split into two at the nine station group dendrogram cutoff.

Conditional probabilities computed at each hierarchical level from 2–8 returned values of $P_m(k)$ that gradually increased in line with the number of station groups and reached a maximum of 0.984 at seven station groups (Fig. 3). A further partition into eight station groups led to a slight reduction in $P_m(k)$, indicating that the within-group association was beginning to weaken. In addition, when the probabilities of the eight station groups were interpolated and the maximum probabilities returned to arrive at a final assemblage map (not shown here), only seven groups were represented. The additional group created by the eight station group cutoff was only represented by a single station, A3, and its probability of membership to this new group was paradoxically lower than that for the dominant group, Group VII. The cutoff at seven station groups (shown in Fig. 2) was therefore used to define the assemblages from the unsupervised classification.

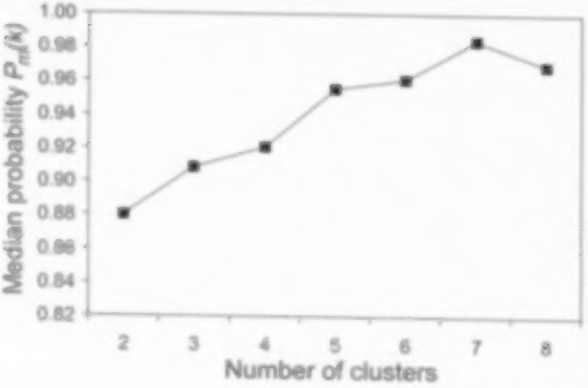


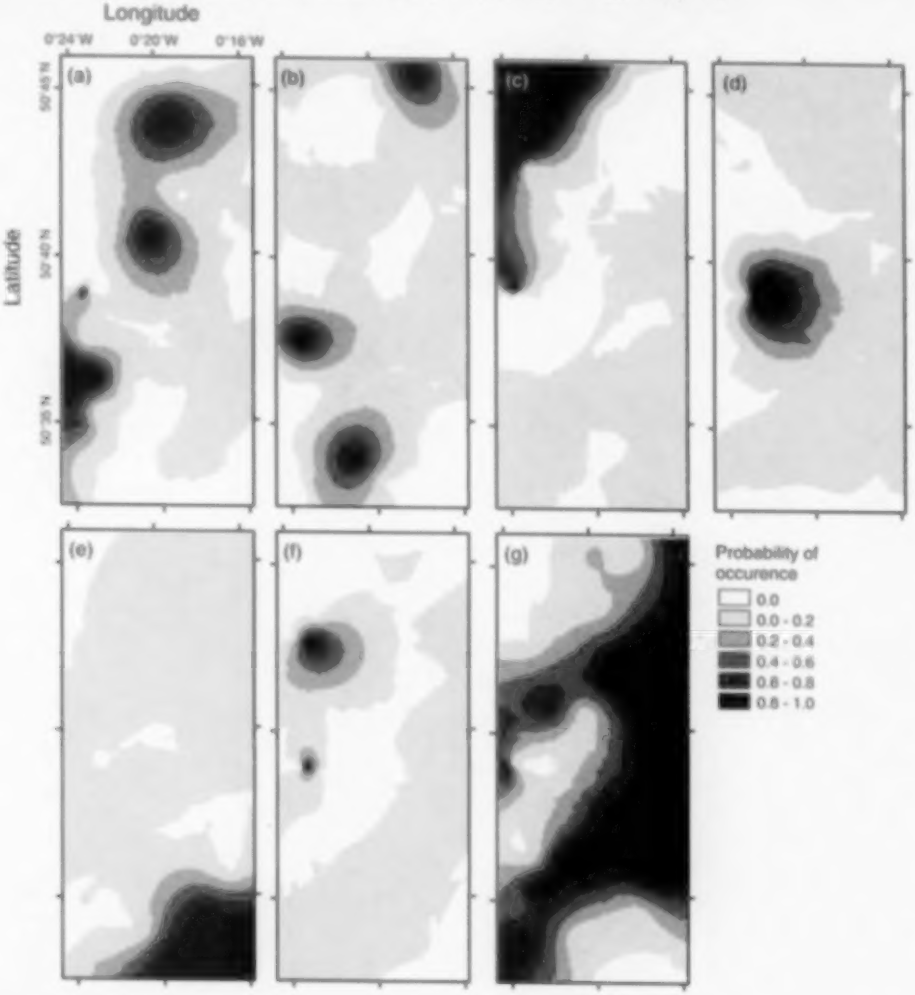
Fig. 3. Median probability $P_m(k)$ for each station group cutoff level, where $P_m(k)$ is calculated from the vector of maximum probabilities at each hierarchical level *k*.

Once the conditional probabilities for the seven station groups had been interpolated over the 10 000 m^2 grid, spatial definition was obtained for the estimated likelihood of occurrence of each assemblage over the study area (Fig. 4). As expected, the Group VII assemblage dominated the site, leaving only three main areas — west–central region, southeast corner, and northwest corner — where the assemblage was unlikely to be present. The Group III, IV, and V assemblages largely mirrored the Group VII assemblage distribution and were associated with a single centre of maximum probability: Group III in the northwest corner, Group IV in the centre of the study area, and Group V in the southeast corner. The Group I, II, and VI assemblages were represented by more than one geographic probability maximum. While some of the biological assemblages were predicted to have a wider spatial distribution compared with others (Group VII in particular), all of the assemblages were found to occur in greater than 50% of the study area, albeit at relatively low levels of probability of occurrence for much of their distribution.

Maps of conditional probabilities for station groups classified in supervised mode showed a less patchy distribution of assemblages compared with those given by the unsupervised classification (Fig. 5). A number of supervised and unsupervised classified assemblages showed broadly similar distributions, most noticeably the Group A and Group V assemblages in the southeast corner of the survey area and the Group H and Group III assemblages in the northwest.

Boundaries given by the map of combined assemblages developed from the unsupervised classification did not generally agree with those associated with the acoustically distinct regions (Fig. 6*a*). There was broad correspondence between the Group III assemblage and acoustic class H and

Fig. 4. Maps showing probabilities of occurrence for each of the station groups from the seven group unsupervised classification: (*a*) Group I; (*b*) Group II; (*c*) Group III; (*d*) Group IV; (*e*) Group V; (*f*) Group VI; (*g*) Group VII.

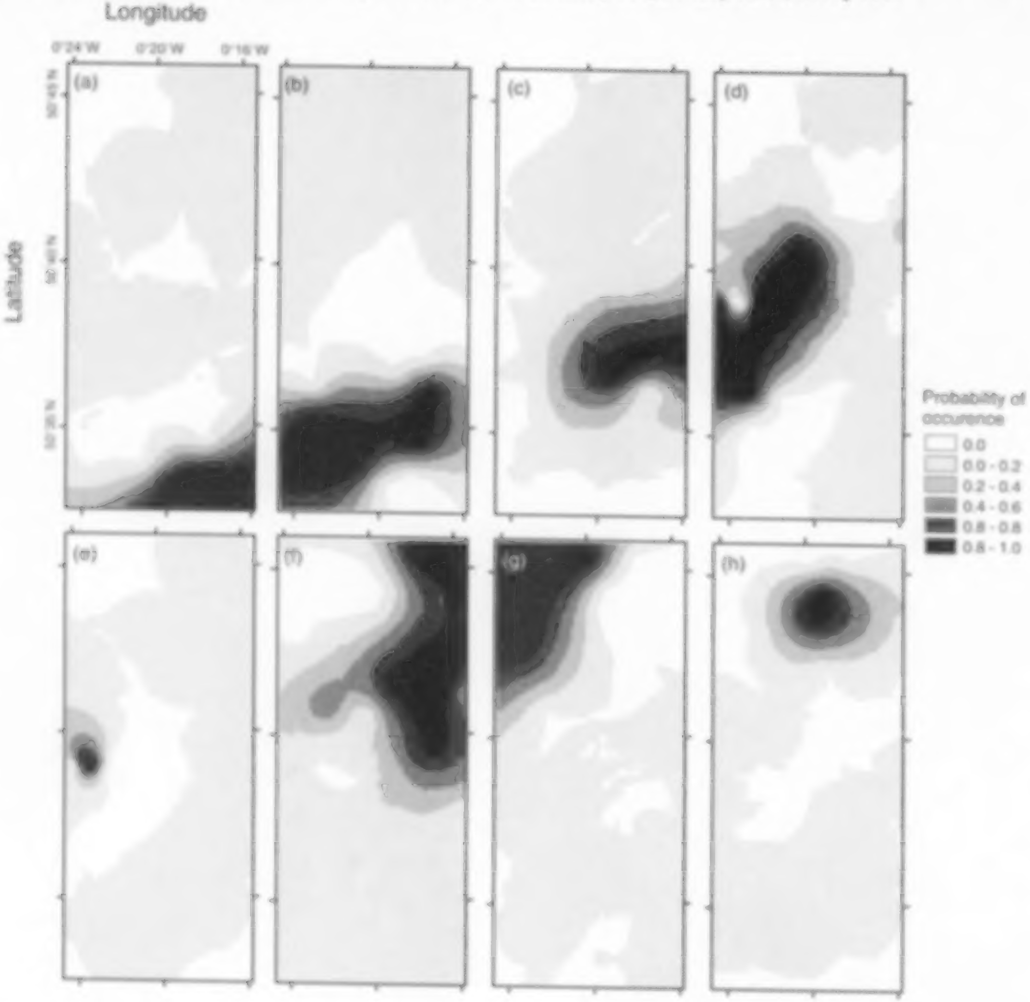


between the Group V assemblage and acoustic class A, thus mirroring the similarity seen between maps of conditional probabilities. The Group VII assemblage dominated much of the study area and cut across five of the acoustic classes.

In contrast with the unsupervised classification, boundaries between the final set of assemblages given by the supervised classification agreed more closely with the boundaries of the acoustically distinct regions (Fig. 6*b*). This outcome, although somewhat expected, is still dependant on the within-group similarity between the stations, which was clearly relatively high. The assemblages given by the supervised classification were also more evenly distributed across the study area and showed a more gradual and even transition in assemblage type from north to south, which is in general agreement with the known physical structure of the seabed across the area (Brown et al. 2002).

The number of indicator species for the assemblages classified in unsupervised mode ranged from zero and two in the Group I and Group VII assemblages, respectively, to a maximum of 10 in the Group IV assemblage (Table 1). Mean indicator values for those species above the 25% threshold ranged between 35% and 50% (average of 43% across all assemblages), suggesting that the assemblages were not tightly defined; by contrast, a more well-defined set of assemblages would have resulted in a higher set of indicator values. Mapped representations of indicator value metrics (total number and mean indicator value) highlighted the variability between assemblages, as well as a clearer separation between the spatially dominant Group VII assemblage, with its low number of indicator species, and assemblages in the central and southeast regions (Groups IV and V) and to a lesser extent with the Group III assemblage in the northwest (Fig. 7.). The Group VII assemblage with its low indicator value metrics is clearly one of the least well-defined of the assemblages. The same is true for the Group I and Group II assemblages, both of which appear to represent transition areas between the dominant Group VII assemblage and those in the extreme northwest and southeast corners. This agrees

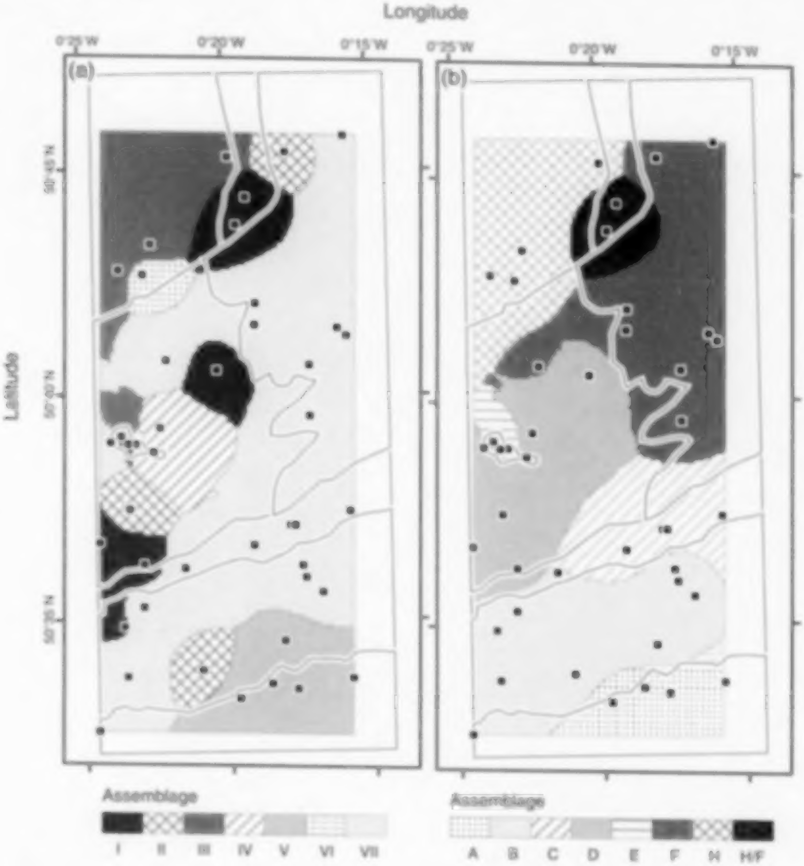
Fig. 5. Maps showing probabilities of occurrence for each of the station groups from the eight group supervised classification: (*a*) Group A; (*b*) Group B; (*c*) Group C; (*d*) Group D; (*e*) Group E; (*f*) Group F; (*g*) Group H; (*h*) Group H/F.



with the known seabed conditions of the study site, where no clear boundaries in the physical seabed characteristics were noted, but where instead substrate types varied gradually (Brown et al. 2002).

Indicator value metrics for the assemblages classified in supervised mode showed a similar level of variation across assemblages to those given by the unsupervised classification (Fig. 7). If the extreme high mean indicator value associated with Group F is ignored (the assemblage was only associated with one indicator species), the maps of indicator value metrics show a broadly similar spatial arrangement to those given by the unsupervised classification. For example, boundaries given by assemblages B, C, and F show a relatively high degree of spatial coincidence with the Group VII assemblage of the unsupervised classification and also have a low or indeterminate number of indicator species and mean indicator value. Similarly, assemblages in the west–central region, northwest corner, and southeast corner are generally associated with higher indicator value metrics in agreement with the equivalent assemblages given by the unsupervised classification. Levels of similarity between indicator species given by the two methods of classification highlighted areas of agreement and disagreement between assemblages (Fig. 8). Assemblages in the southeast corner (unsupervised Group V and supervised Group A) showed strongest agreement, while assemblages in the northwest (unsupervised Group III and supervised Group H) and those in the central region equating to Group VII of the unsupervised classification and Groups B and F of the supervised classification showed average similarity. Large areas of the study region were marked by no apparent similarity in indicator species. The spatial pattern in indicator species metrics and similarity suggests a broad separation of the study area into four relatively distinct zones on the basis of the infaunal assemblages present, which again is in general agreement with the known physical structure of the seabed (Brown et al. 2002). Domi-

Fig. 6. Final assemblage maps developed from (*a*) the seven station groups given by the unsupervised classification and (*b*) the eight station groups given by the supervised classification. Note that similar region symbols between the assemblage maps are not representative of corresponding assemblage types. The boundaries of the acoustically distinct regions are superimposed on both assemblage maps to provide a visual assessment of the level of correspondence between acoustic regions and assemblages. Solid squares are the positions of Hamon grab sample stations.



nating the region is a group of poorly defined assemblages running diagonally between the northeast and southwest corners. This region consists largely of mobile sands or sands over gravel and separates two relatively distinct and well-defined assemblages in the southeast and northwest, both of which are composed of coarser sediments and gravels. The fourth assemblage extends from the western boundary into the central region of the study area and is composed largely of heterogeneous sediments. Between these regions lie areas of transition from the more mobile and mixed sediments in the central areas to the gravels, pebbles, and coarser sediments that characterize the assemblages in the southeast and northwest corners.

Although the assemblages given by the two approaches were found to be broadly comparable in terms of their spatial definition and biological complexes, the unsupervised classification yielded a higher total number of indicator species (Table 1). This approach also gave a slightly higher median conditional probability at the seven group cutoff (0.984) compared with the eight station groups of the supervised classification (0.966). Higher probabilities and indicator values suggest that the unsupervised classification offered a slightly better definition of the assemblages at the study site.

Discussion

The primary objective of this study was to assess whether a bottom-up, unsupervised approach to assemblage classification arrived at a more distinct and better-defined set of assemblages compared with the top-down, supervised classification used by Brown et al. (2002). One issue that must be kept in mind is that in contrast with Brown et al. (2002), we restricted our study to burrowing and infaunal species only, as the main purpose was to assess whether biological assemblage maps given by the two approaches differed. Results given by the bottom-up classification compared with the top-down allocation of stations to assemblages suggests that there was probably little gain in stratifying the sampling design within the eight acoustically distinct regions. A similar spatial separation of assemblages was arrived at when the a

Table 1. Indicator species and taxa for the assemblages defined by the two methods of classification (unsupervised vs supervised) and associated metrics of indicator value (IV), specificity (*S*), and fidelity (*F*).

Assemblage	Species or taxa	IV	*S*	*F*
Unsupervised				
I	None	na	na	na
II	Nemertea	41.2	0.41	1.00
	Owenia fusiformis	34.7	0.52	0.67
	Polycirrus sp.	25.8	0.26	1.00
	Goniadia maculata	35.7	0.54	0.67
	Aonides paucibranchiata	26.3	0.26	1.00
	Spiophanes bombyx	39.7	0.59	0.67
	Maldanidae sp.	38.2	0.38	1.00
		(34.5)		
III	*Terrebellides stromi*	29.8	0.40	0.75
	Polycirrus sp.	27.7	0.28	1.00
	Thelepus cincinnatus	77.3	0.77	1.00
	Heteromastus filiformis	39.6	0.40	1.00
		(43.6)		
IV	*Scalibregma inflatum*	32.7	0.33	1.00
	Amphicteis gunneri	71.9	0.72	1.00
	Poecilochaetus serpens	39.6	0.40	1.00
	Scolelepis squamata	31.3	0.63	0.50
	Caulleriella zetlandica	36.9	0.37	1.00
	Notomastus sp.	37.7	0.38	1.00
	Maldanidae	27.6	0.28	1.00
	Upogebia deltaura	40.9	0.41	1.00
	Urothoe elegans	43.8	0.44	1.00
	Abra prismatica	41.3	0.41	1.00
		(40.4)		
V	*Poecilochaetus serpens*	25.7	0.31	0.83
	Aonides paucibranchiata	55.2	0.55	1.00
	Laonice sp.	81.9	0.98	0.83
	Aphelochaeta sp.	64.8	0.78	0.83
	Notomastus sp.	30.5	0.37	0.83
	Upogebia deltaura	29.3	0.44	0.67
	Ampelisca sp.	35.6	0.36	1.00
	Abra prismatica	34.5	0.41	0.83
		(44.7)		
VI	*Scalibregma celticum*	77.2	0.77	1.00
	Scalibregma inflatum	35.8	0.36	1.00
	Ampharete sp.	48.6	0.49	1.00
	Terrebellides stromi	28.9	0.29	1.00
	Lumbrineris latreilli	41.3	0.41	1.00
	Caulleriella alata	72.8	0.73	1.00
	Heteromastus filiformis	56.3	0.56	1.00
	Notomastus latericeus	58.5	0.58	1.00
	Modiolus sp.	38.1	0.76	0.50
		(50.8)		
VII	*Ophelia limacina*	36.6	0.63	0.58
	Bathyporeia elegans	36.5	0.87	0.42
		(36.5)		
Supervised				
A	*Poecilochaetus serpens*	39.9	0.50	0.80
	Aonides paucibranchiata	53.3	0.53	1.00
	Laonice sp.	96.6	0.97	1.00
	Aphelochaeta sp.	58.2	0.73	0.80
	Notomastus sp.	35.3	0.44	0.80
	Maldanidae	27.7	0.28	1.00
	Upogebia deltaura	32.3	0.54	0.60
	Ampelisca sp.	42.8	0.43	1.00
	Abra prismatica	41.5	0.52	0.80
		(47.5)		
B	*Ophelia limacina*	27.8	0.56	0.50
C	None	na	na	na
D	Maldanidae	32.5	0.32	1.00
	Urothoe elegans	28.0	0.45	0.63
		(30.2)		
E	*Scalibregma celticum*	67.2	0.67	1.00
	Goniadia maculata	28.4	0.43	0.67
	Nematonereis unicornis	27.1	0.41	0.67
	Lumbrineris latreilli	36.5	0.36	1.00
	Caulleriella alata	25.9	0.26	1.00
	Caulleriella zetlandica	37.0	0.37	1.00
	Heteromastus filiformis	52.5	0.79	0.67
	Modiolus sp.	48.5	0.73	0.67
	Abra alba	34.0	0.51	0.67
		(39.7)		
F	*Bathyporeia elegans*	60.8	0.81	0.75
H	*Scalibregma inflatum*	37.2	0.37	1.00
	Terrebellides stromi	50.6	0.67	0.75
	Thelepus cincinnatus	45.1	0.60	0.75
		(44.3)		
H/F	*Owenia fusiformis*	55.4	0.55	1.00

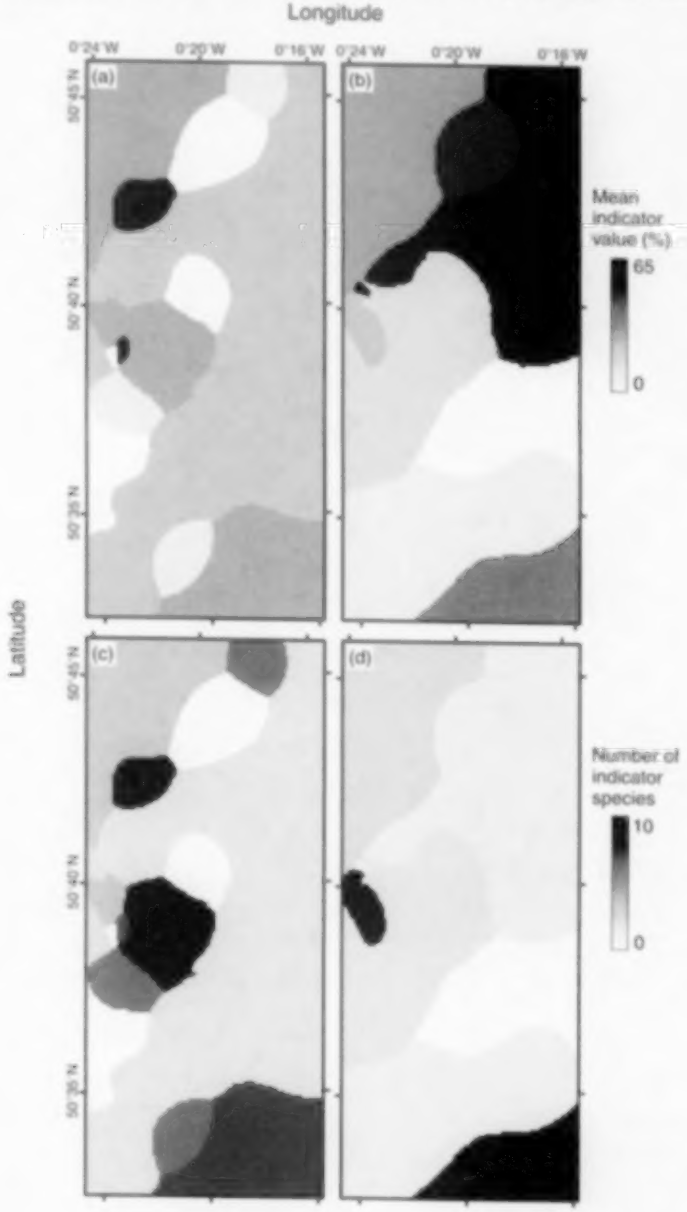
Note: IV is represented as a percentage, whereas *S* and *F* are on a scale of 0–1, where 1 equals maximum specificity or fidelity. Mean assemblage IVs are shown in parentheses where appropriate; na, not applicable.

priori station classification was ignored and the stations were allowed to form groups on the basis of an objective similarity metric.

Despite these differences, the two approaches to classifying biological samples using either a top-down or bottom-up perspective have their own relative merits depending on the type of question being asked. If the purpose of the study is to evaluate the efficacy of acoustic sensors for mapping physical components of the seabed that are then used as proxies for the biological component (through ground-truth sampling), then a sampling program based on the supervised classification of biological samples within acoustically distinct seabed regions is needed. Evaluating acoustic sensors for the purpose of seabed mapping was the main objective of Brown et al. (2002). If, however, the seabed comprises relatively homogenous, unconsolidated sediments and the main driver is the development of the best possible biological assemblage map, then a bottom-up, unsupervised approach is likely to arrive at a set of assemblages that are defined equally well or slightly better compared with a top-down approach. Similar findings have recently been reported by Hewitt et al. (2004), although the authors found a clearer distinction between the two approaches, possibly because the bottom-up approach incorporated both acoustically derived physical attributes alongside the biological data.

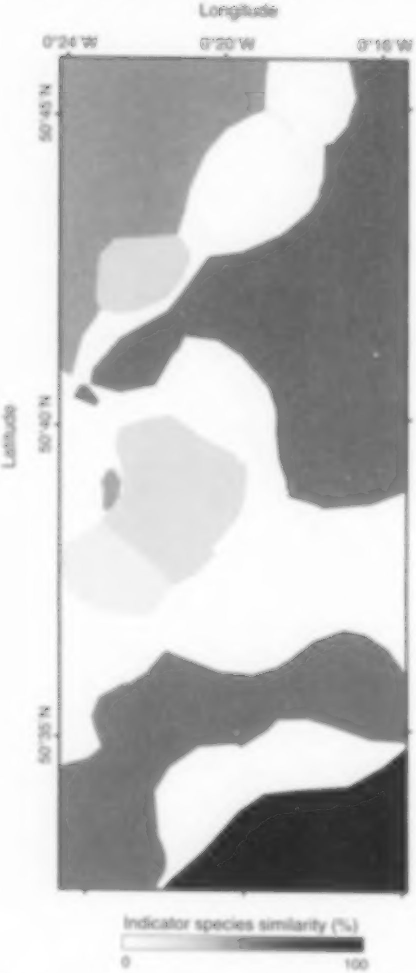
When developed using the bottom-up classification, the final map of combined assemblages contained boundaries

Fig. 7. Final assemblage maps from Fig. 6 showing mean indicator values and number of indicator species per habitat type: (*a*, *b*) mean indicator values for the seven group unsupervised classification and eight group supervised classification, respectively; (*c*, *d*) number of indicator species for the seven group unsupervised classification and eight group supervised classification, respectively.



that do not generally agree with those associated with the acoustically distinct regions, despite some localized similarities. While acoustic systems can rapidly collect physical data over large areas of seabed, they are unable to detect changes in biological components except in cases where the physical structure is modified by the associated biota in such a way as to produce relatively distinct spatial demarcations, for example through localized biogenic accumulation, e.g., mussels, maerl, or reef development (Kenny et al. 2003). By contrast, discrete biological sampling will be unable to detect sharp gradients and discontinuities in the physical structure of the seabed unless sampling intensity is relatively high. In the present study, a few of the assemblages were only represented by a small number of stations (three or fewer), and sampling intensity was relatively low over the entire area. Both aspects of the sampling design will reduce the possibility of detecting sharp gradients and change between assemblages if considered in isolation of physical seabed conditions. Given the relatively homogenous character of the seabed in the study area, it is unsurprising that the two methods produced

Fig. 8. Level of similarity between indicator species given by the supervised and unsupervised classification methods. Similarity is represented as a percentage of the total number of indicator species between spatially coincident assemblages.



assemblages with a different set of boundaries. Hence, a bottom-up classification based on combined acoustic and biological attributes may instead offer the best solution to mapping seabed biotopes (physical + biological), as the advantages of both data collection methods for seabed mapping would be used to best effect (Hewitt et al. 2004).

One of the additional benefits of the mapping approach described here was that it gave some information on how well the boundaries of the biological assemblages compared with the acoustically distinct substrates. Patterns of community distribution in relation to physical seabed conditions could thus be determined simply by cross-comparing boundaries. The maps of conditional probabilities suggested that relationships between assemblages and physically defined acoustic regions gradually weaken in areas of transition between different physical environments and strengthen with increasing distance from transition zones. Transition zones could, however, equally support relatively well-defined assemblages. Relationships between physical environments and seabed fauna can only be better understood if we have a fixed reference system for classifying assemblages and physical environments, and as this study and others have shown, both can be classified in many different ways. In the UK and elsewhere, there are major ongoing efforts to develop standard classifications for biological assemblages, physical environments, and biotopes (e.g., Connor et al. 2004; Davies et al. 2004; Madden and Grossman 2004). Widely accepted systems of classification and targeted sampling programs will form the basis for better understanding spatial variations in the strength of the relationship between benthic communities and physical seabed attributes.

The method described here offers a relatively straightforward solution to mapping individual assemblages as continuous distributions rather than simply as discrete entities with hard boundaries. While the distribution of an individual assemblage is easily estimated and visualized in geographic space by interpolating the conditional probabilities, attempting to map all probabilities for individual assemblages will result in a visually confused representation of assemblage spatial structure that would be difficult to interpret. Consequently, there would be few advantages over the more common type of assemblage map where individual assemblages are represented as homogenous units with discrete boundaries. A recent study by Urbański and Szymelfenig (2003) provides a good example of this. Their habitat map of the Polish zone of the Baltic Sea consists of nine primary habitat types, which in turn are further defined by varying combinations of 23 subtypes. The map is easily interpretable in terms of the nine primary habitat types, but not so for the 23 habitat subtypes. This highlights the problems of visually interpreting complex environmental information through the medium of a static map.

A crucial element to the bottom-up approach to assemblage classification is an objective means to decide the level at which to cut the dendrogram and thus define groups of similar biological complexes. A slightly different cutoff can yield a very different set of assemblages. We adopted the approach suggested by Souissi et al. (2001) to examine median probabilities $P_m(k)$ given by each hierarchical level and assigned the cutoff to the level where $P_m(k)$ was at a maximum. Souissi et al. (2001) similarly found $P_m(k)$ to increase with each successive higher-order level, but instead assigned the final cutoff to the first partition that exceeded a median probability of 0.95. If the same criteria had been adopted here, the cutoff would have been set at five station groups. Interestingly, the assemblage map resulting from this partition (not shown here) did not differ substantially from the seven station group partition explored in detail in this study. With this in mind, we recommend that future studies adopt the $P_m(k) = 0.95$ criteria as an objective means for deciding on the dendrogram partition level.

In conclusion, our study found that when mapping assemblages over relatively homogenous areas of seabed that consist predominantly of gravels and sands, the use of an unsupervised approach arrived at a slightly more well-defined set of assemblages compared with an a priori classification given by a visual interpretation of acoustic seabed data. Biological sampling is more time-consuming compared with acoustic surveying, and based on the outcome of this study, a map developed from biological sampling alone did not produce results that were markedly superior to the equivalent map based on acoustic interpretation. These factors will influence the method selected when mapping over large spatial areas. Also, in areas of seabed characterized by a high degree of substrate heterogeneity, maps produced from biological sampling alone will be less able to detect changes in community structure over small spatial scales. Acoustic surveying, by comparison, can be more cost-effective when surveying large areas of seabed and is better able to detect sharp gradients in seabed structure and composition. Given the comparable results of the two methods of classification applied to the study area, the choice of approach for future mapping exercises depends on resource constraints and the level of precision required in the final biological assemblage map. Further testing in different seabed environments will allow a more thorough assessment of the relative merits of the two approaches and their application to classifying a more diverse set of benthic assemblages.

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Changes in spring phytoplankton communities and nutrient dynamics in the eastern basin of Lake Erie since the invasion of *Dreissena* spp.

Richard P. Barbiero, David C. Rockwell, Glenn J. Warren, and Marc L. Tuchman

Abstract: Distinct changes have occurred in the size and composition of the spring phytoplankton community in the eastern basin of Lake Erie following the introduction of *Dreissena*. Since 1996, total phytoplankton biovolume has decreased to approximately 20% of pre-*Dreissena* levels, whereas postinvasion concentrations of spring soluble nutrients, particularly silica, have been substantially elevated compared with earlier years. Spring dominance has shifted from a mix of pennate and large centric diatoms and pyrrophytes to three centric diatoms with high silica requirements: *Aulacoseira islandica*, *Stephanodiscus hantzschii*, and *Stephanodiscus parvus*, and the overall diversity and species richness of the spring phytoplankton community has declined significantly. In addition, current April silica concentrations are approximately twice as high as historical (i.e., 1960s–1980s) winter maxima, indicating that the silica content of the lake has increased since the dreissenid invasion. These results suggest that the severe silica depletion caused by increased anthropogenic inputs of nutrients during the last century has been mitigated through a decrease in diatom production, most likely brought about by dreissenid grazing.

Résumé : Il s'est produit de nets changements dans la taille et la composition de la communauté printanière de phytoplancton dans le bassin oriental du lac Érié depuis l'introduction de *Dreissena*. Depuis 1996, le biovolume total du phytoplancton a décru jusqu'à environ 20 % des valeurs pré-*Dreissena*, alors que les concentrations de nutriments solubles au printemps, particulièrement de la silice, se sont accrues substantiellement après l'invasion par comparaison aux années antérieures. La dominance au printemps a changé d'un mélange de diatomées pennées et centriques de grande taille et de pyrrhophytes à une dominance de trois diatomées centriques, *Aulacoseira islandica*, *Stephanodiscus hantzschii* et *Stephanodiscus parvus*, à forts besoins en silice; la diversité globale et la richesse spécifique de la communauté printanière de phytoplancton ont diminué de façon significative. De plus, les concentrations actuelles de silice en avril sont approximativement deux fois plus élevées que les maximums hivernaux du passé (i.e., les années 1960–1970), ce qui montre que le contenu en silice du lac a augmenté depuis l'invasion des dreissénidés. Ces résultats indiquent que la réduction importante de silice due à l'accroissement des apports anthropiques de nutriments au cours du siècle dernier a été mitigée par un déclin de la production de diatomées très probablement causé par le broutage des dreissénidés.

[Traduit par la Rédaction]

Introduction

Suspension feeding bivalves can exert a controlling influence on primary producers in coastal and estuarine aquatic systems (Carlson et al. 1984; Gerritsen et al. 1994). Such impacts had not been seen in freshwater systems in North America until the appearance of dreissenid mussels. Because of their characteristically high filtration rates and their potential to form extremely dense populations, dreissenids can significantly lower phytoplankton biomass in a variety of systems. Such declines have been seen in the nearshore (Nicholls and Hopkins 1993) and offshore (Leach 1993; Barbiero and Tuchman 2004) of Lake Erie, in Saginaw Bay, Lake Huron (Fahnenstiel et al. 1995), in the Hudson River (Caraco et al. 1997), and in Oneida Lake, New York (Idrisi et al. 2001). Theoretically, mussels can also produce shifts in phytoplankton community composition through a number of direct and indirect mechanisms. A high degree of selectivity of captured particles has been shown to take place within the mantle cavity of *Dreissena*, with rejected materials ejected as pseudofeces through the exhalant siphon (Baker et al. 2000; Ten Winkel and Davids 1982). If resuspended, algal cells contained in these pseudofeces could theoretically continue growth in the water column. Similarly, differential resistance to digestion could also promote shifts towards more resistant algal species if feces are resuspended.

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In the absence of selective removal, alterations in nutrient or light regimes resulting from filtration activities could change competitive outcomes between species, for instance by lowering N:P ratios (Arnott and Vanni 1996), thus favoring species with superior competitive abilities for N (Smith 1982). Also, nonselective filtration could favor phytoplankton with higher growth rates or those that can minimize spatial overlap with the benthic mussels, e.g., through buoyancy mechanisms (MacIsaac 1996).

In spite of these potential mechanisms to alter phytoplankton community structure, to date there have been few unambiguous reports of species-level shifts in phytoplankton communities following dreissenid invasions. Based on 2 years of preinvasion data and 4 years of postinvasion data, Smith et al. (1998) documented a decline in relative cyanobacteria (mostly *Microcystis*) abundance and an increase in diatom abundance after the *Dreissena* invasion of the Hudson River. In contrast, diatom populations in Oneida Lake, New York, seem to have declined after the dreissenid invasion (Idrisi et al. 2001). There is also some anecdotal evidence suggesting that dreissenid grazing might have increased the frequency of *Microcystis* blooms in Saginaw Bay, Lake Huron, and the western basin of Lake Erie (Vanderploeg et al. 2001). In contrast, though, Nicholls and Hopkins (1993) showed that dreissenid grazing had equal impacts across all phytoplankton groups in nearshore regions of Lake Erie.

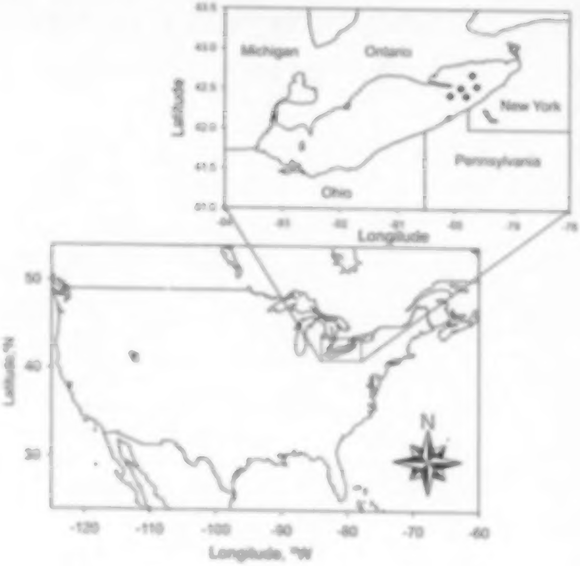
Previous studies from our program examining the immediate postdreissenid years in the eastern basin of Lake Erie have found increases in soluble phosphorus and silica (Makarewicz et al. 2000) but no changes in phytoplankton biovolume (Makarewicz et al. 1999). However, both direct (Patterson et al. 2005) and indirect (Barbiero et al. 2006) evidence suggest that *Dreissena* populations in the eastern basin have increased substantially since the early 1990s, and therefore identifying dreissenid-related impacts on the open waters of Lake Erie might require a longer-term data set. Here we utilize a data set that extends more than a decade past the initial *Dreissena* invasion to discern direct and indirect impacts of dreissenids on water chemistry and phytoplankton assemblages in eastern Lake Erie.

Materials and methods

The data used in this study come from the annual monitoring program of the US Environmental Protection Agency's Great Lakes National Program Office (GLNPO). The data set extends from 1983, the initial year of monitoring, to 2000, the most recent year for which phytoplankton data are available. Sampling was conducted during the spring isothermal period (generally April) and the summer stratified period (August) at five offshore stations (not all stations were sampled in all years) in the eastern basin of Lake Erie (Fig. 1). Station depths ranged from 32 m to 60 m. Spring survey dates ranged from 1 April to 9 May, with the exception of 1999 when the cruise on Lake Erie was unusually early (10 March). Summer sampling dates ranged from 2 August to 22 August.

At each station, both discrete and composite samples were taken with Niskin bottles mounted on a Sea-Bird Carousel Water Sampler (Sea-Bird Electronics Inc., Bellevue, Washington). Composite samples for spring phytoplankton analyses were composed of equal aliquots collected from 1, 5, 10, and 20 m. Samples for total soluble phosphorus (TSP) and soluble silica (Si) were filtered in the field through 0.45 µm filters (Sartorius AG, Goettingen, Germany). Samples for TSP and total phosphorus (TP) were preserved with H_2SO_4 for later analysis in the lab. Samples for soluble Si were stored at 4 °C. Samples for phytoplankton analysis were preserved with Lugol's solution in the field and with formalin upon return to the laboratory.

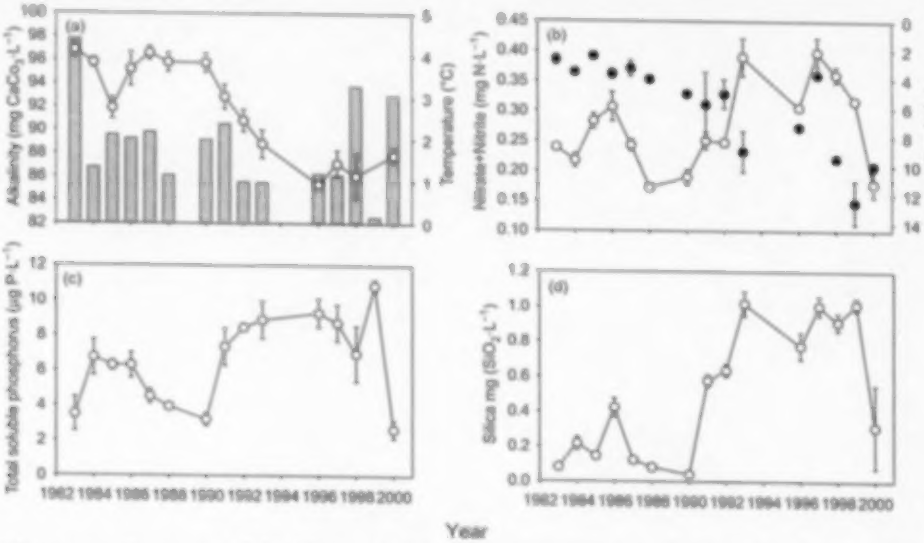
Fig. 1. Map of Lake Erie showing locations of sampling stations. Not all stations were sampled in all years.



TSP and TP were measured on a Lachat QuikChem AE autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin) by the ascorbic acid method after acid persulfate digestion (American Public Health Association (APHA) 1985). Soluble Si was determined as SiO_2 by the molybdate method on a Lachat QuikChem AE autoanalyzer (APHA 1985). Before 1991, chemical analyses were conducted on board ship; after this date, analyses were performed in a land-based laboratory. Internal comparisons have shown no difference and confirmed the comparability of data from the two periods (G.J. Warren, unpublished data).

Phytoplankton abundances were estimated, and *Urosolenia* (= *Rhizosolenia*) species and all nondiatom phytoplankton were identified, using the Utermöhl technique (Lund et al. 1958) at a magnification of 500×, with diatoms other than *Urosolenia* identified as either centrics or pennates at this stage. At least 250 individuals were enumerated along parallel transects across the middle of the chamber. Identification of diatoms (aside from *Urosolenia*) was done from permanent slide mounts at 1250×, with approximately 500 frustules identified per sample. Relative proportions of each taxon of centrics and pennates were then multiplied by the appropriate Utermöhl counts. At least 10 individuals of each taxon were measured per sample, and cell volumes were computed using appropriate geometrical formulae. Biovolume was used as the fundamental response variable in all statistical analyses. To minimize the effects of

Fig. 2. Annual basin-wide averages of spring (*a*) alkalinity (open symbols) and temperature (vertical bars), (*b*) Secchi depth (solid symbols; replotted from Barbiero and Tuchman 2004) and nitrate and nitrite nitrogen (open symbols), (*c*) total soluble phosphorus, and (*d*) soluble silica. Whiskers represent ±1 SE.



changes in analyses over the course of the 17-year data set, diatom taxa were lumped to species (original identifications were often at the level of variety) and nondiatom taxa were lumped to genus. In the case of particularly ambiguous groups, such as some colonial coccoid cyanobacteria, higher level lumping occurred.

The data set was divided into three periods: predreissenid (1983–1990), an immediate postinvasion period (1991–1993), and a later postinvasion period (1996–2000). The rationale for this division of the data set is provided below (see Results). Patterns in community data were analyzed using detrended correspondence analysis (DCA; Hill and Gauch 1980), with a square-root transformation applied to the biovolume data before analysis. Although samples in our data set were collected over a relatively narrow range of dates, slight systematic differences in the timing of seasonal succession from year to year, resulting from interannual climatic differences or variations in the timing of cruises, could potentially result in apparent patterns in phytoplankton communities not due to dreissenid effects. Therefore, to remove the influence of any such interannual differences, seasonal effects were partialed out of the DCA (ter Braak and Prentice 1988) by incorporating water temperature into the analysis as a covariable. The resulting ordination presents residual patterns in phytoplankton community composition after any potential effects of temperature were removed. As an additional, computationally independent assessment of the relatedness of different phytoplankton communities, hierarchical agglomerative cluster analysis using group-average linking was conducted on Bray–Curtis similarities, calculated between all spring phytoplankton samples after a square-root transformation. To test for differences in community composition between the three dreissenid periods, an analysis of similarities (ANOSIM, a multivariate analogue of analysis of variance (ANOVA)) was used (Clarke and Green 1988). This analysis is based on a nonparametric permutation procedure applied to a rank similarity matrix. A Bray–Curtis similarity matrix was derived from all possible combinations of samples, and the resulting similarity ranks were analyzed as for a two-way, nested design, with dreissenid period a three-level main factor (predreissenid period, immediate postinvasion period, later postinvasion period), and year nested within the main factor levels. The resulting statistic, *R*, theoretically ranges from –1 to 1 and is associated with a probability derived from the simulated test statistic distribution expected under the null hypothesis. To help identify which species were most responsible for any observed differences between different dreissenid periods, an index comprised of the average contribution of individual species to between-group Bray–Curtis dissimilarities (δ), divided by the standard deviation of those dissimilarities, was calculated (Clarke 1993). Species for which this ratio is high contribute the most towards discriminating between two groups of samples. Differences between dreissenid periods were also assessed for diversity, evenness, and species richness using a generalized linear model, with dreissenid period a three-level main factor and year nested within period. In the case of a significant main factor effect, differences between periods were assessed using Tukey's honestly significant difference (HSD). The diversity of phytoplankton communities was calculated using the Shannon–Wiener H' index:

$$(1) \qquad H' = -\sum_{i=1}^{n} p_i \log p_i$$

where p_i is the proportion of individuals occurring in species i.

Evenness was calculated as

$$(2) \qquad J = \frac{H'}{H_{\max}}$$

where $H_{\max}$ = log(species number).

Nutrient optima and tolerances of dominant species were calculated using weighted averaging, and standard errors of

Fig. 3. Depth profiles of soluble silica (open symbols) and temperature (solid symbols), taken at the deepest point in the eastern basin of Lake Erie, for cruises undertaken between April 1983 and April 1984. Broken lines indicate average April 1983 soluble silica concentration.

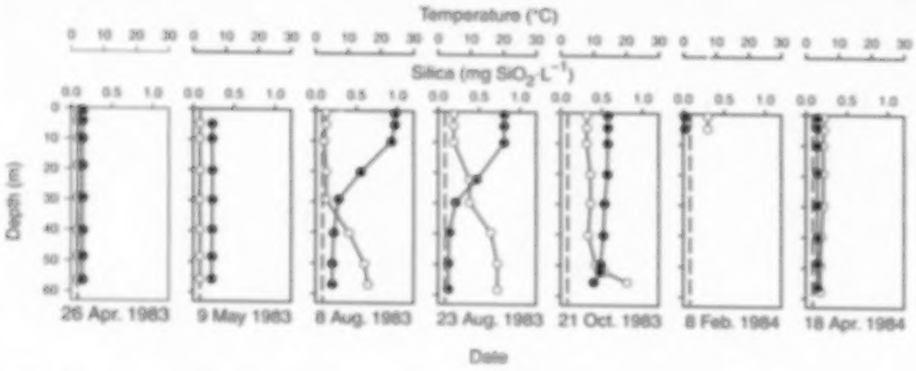
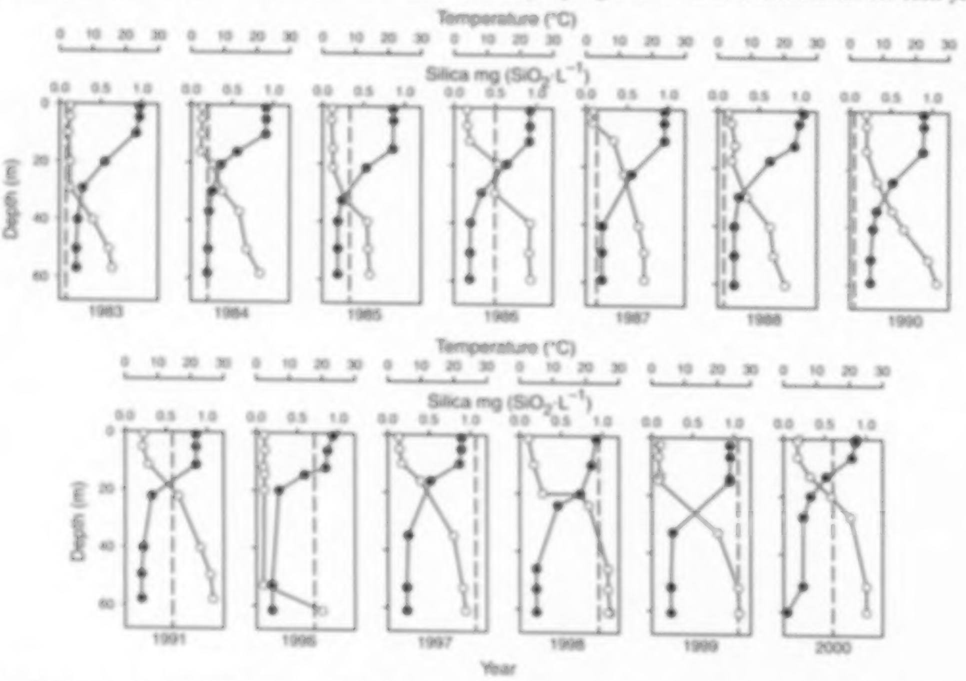


Fig. 4. Depth profiles of soluble silica (open symbols) and temperature (solid symbols), taken at the deepest point in the eastern basin of Lake Erie, for August cruises, 1983–2000. Broken lines indicate average spring soluble silica concentrations for each year.



optima were estimated with bootstrapping, using the program C2 (Juggins 2003). Because of data input limitations of the program, only one cruise per year was used in this analysis, in all cases the spring cruise with a sampling date most closely approaching the overall average sample date.

Results

Physical and chemical

Spring alkalinity exhibited a clear decline beginning in 1991, decreasing from approximately 95 mg CaCO$_3$·L^{-1} to about 86 mg CaCO$_3$·L^{-1} by 1996, after which levels stabilized (Fig. 2a). We have hypothesized (Barbiero et al. 2006) that this decrease in alkalinity was due to calcium uptake by burgeoning dreissenid populations in the eastern basin of Lake Erie and, therefore, that the trajectory of changes in alkalinity can be taken as an indication of dreissenid population growth and hence the potential magnitude of dreissenid effects in the basin. If our alkalinity data are interpreted in this way, then *Dreissena* effects in the basin might be expected as early as 1991, whereas full effects might not appear until after 1993. There is a gap in our data between 1993 and 1996, and it is at some point between these two years that the decline in alkalinity ceased, signaling a moderation in the rate of dreissenid population expansion. Complete time series data of dreissenid population development in Lake Erie are not available. The most extensive report of dreissenid abundances in the eastern basin of Lake Erie dur-

Table 1. Least squares regression results and associated analysis of variance between spring temperature and soluble silica for the predreissenid period 1982–1990 (adjusted $r^2 = 0.06$) and the postinvasion period 1991–2000 (adjusted $r^2 = 0.27$).

Predictor	Coefficient	Standard error	*t* ratio*	*p*	Source	df	SS	Mean square	*F* value	*p*
1982–1990										
Intercept	0.2194	0.03607	6.083	<0.001	Regression	1	0.07170	0.071670	4.495	0.038
Temperature	–0.03159	0.01490	–2.120	0.038	Residual	56	0.8932	0.01595		
					Total	57	0.9649			
1991–2000										
Intercept	0.9967	0.05729	17.40	<0.001	Regression	1	0.7997	0.7997	18.03	<0.001
Temperature	–0.1311	0.03087	–4.246	<0.001	Residual	46	2.040	0.04435		
					Total	47	2.840			

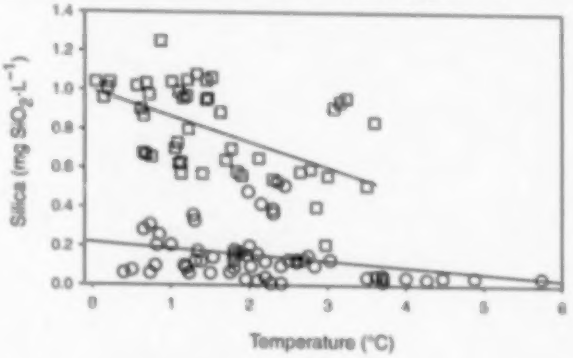
*H_0: $\beta = 0$.

ing the period of our study is that of Jarvis et al. (2000). In that report, total dreissenid biomass (wet weight with shell) from offshore (>30 m depth) stations within our study area were 83 g wet weight·m^{-2} (standard error (SE) = 42, $n = 8$) in 1992, 390 g wet weight·m^{-2} (SE = 111, $n = 2$) in 1993, and 730 g wet weight·m^{-2} (SE = 67, $n = 5$) in 1998. These data are not inconsistent with our interpretation of the alkalinity trends. Therefore, in lieu of more detailed time series census data of dreissenid populations, phytoplankton analyses were divided into three periods, based on our alkalinity data: a predreissenid period of 1983–1990; an immediate postinvasion period of 1991–1993; and a later postinvasion period of 1996–2000.

Average spring cruise water column temperatures were confined to a relatively narrow range (approximately 1–2.4 °C), with notable exceptions being 1983, 1998, and 2000 when temperatures were unusually high and 1999 when, as noted, the spring cruise was undertaken unusually early and consequently the temperature was unusually low (Fig. 2*a*). As we reported elsewhere (Barbiero and Tuchman 2004), Secchi depth showed a tendency to increase subsequent to the appearance of dreissenids, pointing to an improved light climate after the invasion (Fig. 2*b*). Measured soluble nutrients followed a pattern roughly inverse to that of alkalinity, increasing between 1991 and 1993 and then stabilizing somewhat after this point (Figs. 2*b*, 2*c*, 2*d*). This pattern was particularly clear in the case of soluble silica, which showed an immediate and substantial increase that was sustained throughout most of the postinvasion period (Fig. 2*d*). Concentrations of all three nutrients declined abruptly in 2000, probably in part a result of the unusually warm temperatures and presumably enhanced biological activity seen in that year.

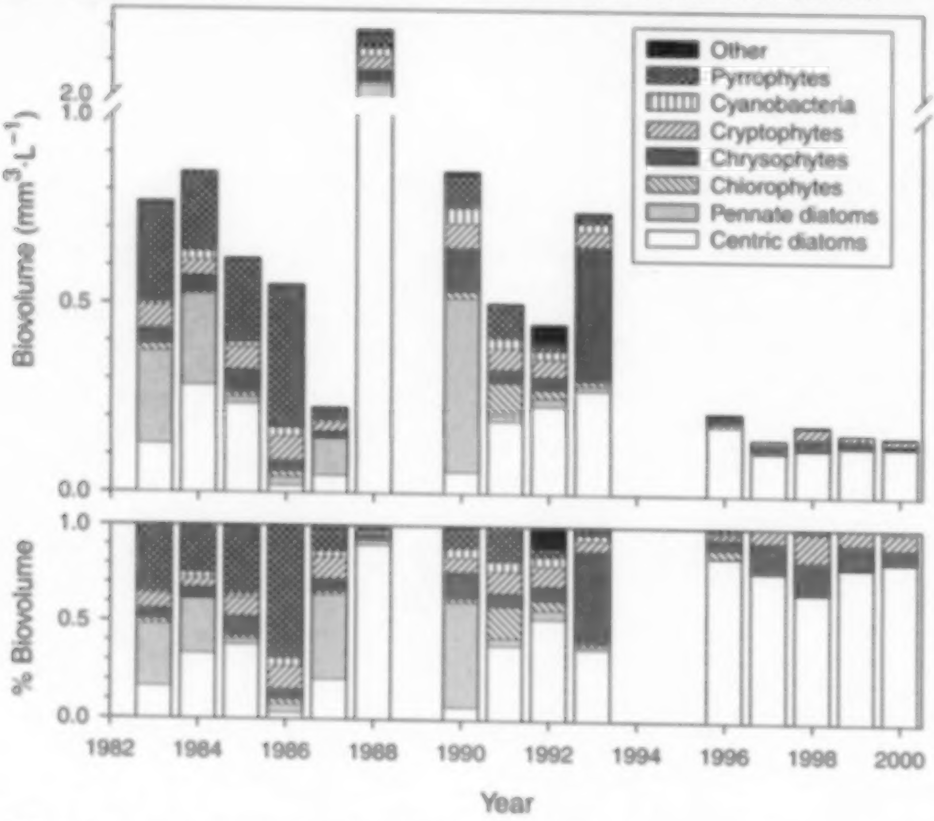
An indication of pre-*Dreissena* silica dynamics is provided by a series of seasonal profiles taken during the early years of the GLNPO program when cruises were undertaken with greater frequency. Profiles from late April 1983 show SiO_2 concentrations on the order of 0.08 mg SiO_2·L^{-1} throughout the water column, with similar concentrations seen 2 weeks later (Fig. 3). Epilimnetic concentrations in early August were essentially unchanged from spring, although hypolimnetic concentrations had increased to 0.4–0.6 mg SiO_2·L^{-1}, which suggests that some resolubilization had taken place. In fact, by mid-August, the silica content of the hypolimnion had increased markedly, and elevated concentrations in the epilimnion compared with the early August date suggest some upward transport. By the next sampling date in late October, the water column had largely destratified, and mixing had increased epilimnetic concentrations to 0.32 mg SiO_2·L^{-1}. Surface concentrations in February were only slightly lower than this (0.30 mg SiO_2·L^{-1}), suggesting minimal uptake between the two sampling dates. The extremely low concentration seen in late April and the minimal difference between that value and August epilimnetic values suggest that most seasonal silica uptake had occurred during the isothermal period. With some exceptions (1985, 1986), this pattern was repeated during the predreissenid period (Fig. 4); spring concentrations averaged 0.23 mg SiO_2·L^{-1} during this time, and August epilimnetic concentrations were usually only slightly lower (average = 0.15 mg SiO_2·L^{-1}). Hypolimnetic silica concentrations were consistently higher than spring concentrations, often substantially so, indicating some degree of resolubilization during the stratified period.

Fig. 5. Relationship between soluble silica and temperature for predreissenid years (1983–1990; ○) and postinvasion years (1991–2000; □), as estimated by least squares regression.



This pattern changed considerably in the postinvasion period, during which April silica concentrations in all years were notably higher than epilimnetic August concentrations (Fig. 4), indicating that a greater amount of silica uptake had taken place between April and August compared with in the preinvasion period. In fact, April silica concentrations after the dreissenid invasion were higher than had been seen at any point in the preinvasion period, averaging 0.76 mg SiO_2·L^{-1}. Data addressing silica winter maxima from our program are limited to cruises and helicopter surveys undertaken in February and December of 1984 and January, February, and November of 1985, from which no values greater

Fig. 6. Spring phytoplankton biovolume, and percent biovolume in the eastern basin of Lake Erie, 1983–2000, by major taxonomic group, averaged from all available spring cruises in each year. Samples were not collected in 1989, 1994, or 1995.



than 0.32 mg $SiO_2 \cdot L^{-1}$ were reported. Therefore, the post-dreissenid period saw not only a reduction in spring silica uptake, but also an increase in the overall silica content of the eastern basin. August epilimnetic concentrations were essentially unchanged from the preinvasion period (average = 0.15 mg $SiO_2 \cdot L^{-1}$).

Typically, as the growing season progresses and surface waters warm, soluble nutrient concentrations would be expected to decrease as a result of uptake by increasing phytoplankton populations. Our silica data suggest that after the dreissenid invasion, spring uptake was reduced. This is reflected in a change in the relationship between temperature and soluble silica concentration since the *Dreissena* invasion (Fig. 5; Table 1). Although silica data from both pre- and post-invasion periods show the expected negative relationship with water temperature, during the pre-*Dreissena* period this relationship was weak ($r^2 = 0.06$) and silica values were low even at the lowest temperatures encountered. Concentrations only decreased slightly at higher temperatures, indicating that a substantial amount of silica uptake had already occurred by the earliest (i.e., coldest) sampling dates, as was also suggested by our silica profile data. The postinvasion relationship between temperature and silica differed significantly from the preinvasion relationship (H_0: $\beta_{\text{preinvasion}} = \beta_{\text{postinvasion}}$, $t = 5.33$, $p < 0.001$), suggesting a "pushing back" of spring silica uptake, with soluble silica concentrations

Fig. 7. Results of detrended correspondence analysis of spring phytoplankton communities in the eastern basin of Lake Erie, with temperature incorporated into the analysis as a covariable. Symbols indicate three groupings: predreissenid period (1983–1990, □); early postinvasion period (1991–1993; △), and later postinvasion period (1996–2000; ○). Samples were not collected in 1989, 1994, or 1995.

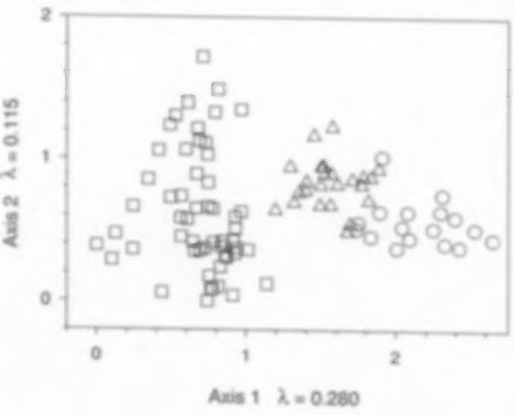
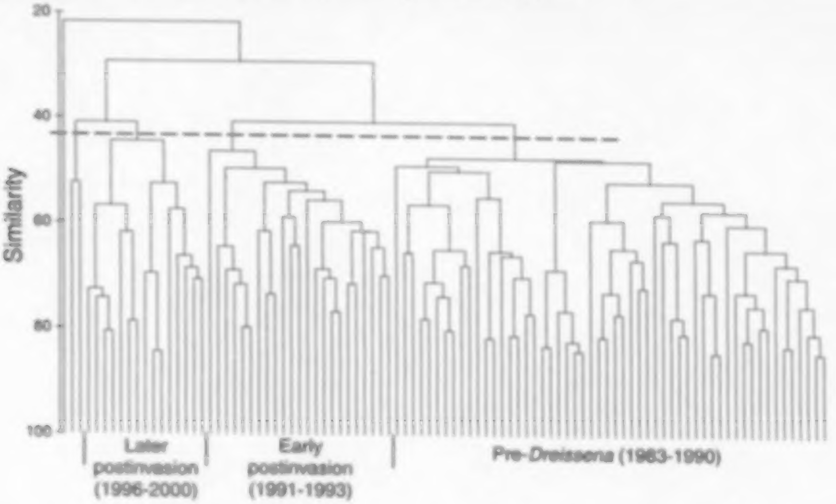


Fig. 8. Dendrogram using group-average linking on Bray–Curtis similarities between spring phytoplankton communities from the eastern basin of Lake Erie. Groups are defined at an arbitrary similarity level of 42%.



much higher at colder water temperatures (1–2 °C) than had been seen in preinvasion years. Even at relatively high (i.e., 3–4 °C) temperatures, soluble silica concentrations were substantially higher than had been seen on any cruise during the predreissenid period, suggesting that diatom populations had not developed sufficiently by the time of the cruise to have resulted in substantial silica draw down.

Phytoplankton community

The spring phytoplankton community, when examined at a gross taxonomic level, exhibited a high degree of variability during the pre-*Dreissena* (1983–1990) period, with pyrrophytes, pennate diatoms, and (or) centric diatoms figuring prominently in different years (Fig. 6). Biovolume during this period varied by nearly an order of magnitude, although this was in a large part due to unusually high numbers of the large-celled centric diatom *Stephanodiscus niagarae* in 1988. During the immediate postinvasion period (1991–1993), centric diatoms contributed more consistently to total phytoplankton biovolume, whereas the importance of pennate diatoms and pyrrophytes was notably diminished. By 1996, phytoplankton biovolume decreased substantially compared with previous years. Between 1996 and 2000, total phytoplankton biovolume was, on average, 20% of pre-*Dreissena* levels, and communities were consistently dominated by centric diatoms, which contributed an average of 78% of biovolume compared with an average of 30% between 1983 and 1990. Chrysophytes were the second most dominant group during the later period, contributing on average 11% of biovolume, whereas cryptophytes made up 8% of postinvasion communities, a contribution that was virtually unchanged from pre-*Dreissena* years. From 1996 to 2000, phytoplankton communities exhibited a notable degree of consistency, in terms of both total biovolume and gross taxonomic composition.

Phytoplankton communities were ordinated using a detrended correspondence analysis in which possible seasonal effects were removed by inclusion of water temperature as a covariable. The first two ordination axes explained 39.5% of the variation in the species data; the total inertia of the analysis was 1.533. The ordination resulted in a complete separation of pre- (1983–1990) and post- (1991–2000) invasion communities, with this separation taking place entirely on the primary ordination axis (Fig. 7). The further division into early (1991–1993) and later (1996–2000) postinvasion periods, suggested by the chemical data, was corroborated by the ordination, in which communities from these two periods were almost completely separated, again on the primary ordination axis. Agglomerative cluster analysis provided an additional, independent confirmation of this division of phytoplankton communities into three distinct periods (Fig. 8). Ignoring three outliers (one sample each from 1992, 1996, and 2000), the first branch in the cluster dendrogram (similarity = 29.3) split 1996–2000 communities from 1983–1993 communities; 1983–1990 and 1991–1993 communities were separated at the next branch (similarity = 40.7). Statistical testing for differences in phytoplankton communities between the three dreissenid periods using the ANOSIM procedure resulted in a highly significant main factor effect (R = 0.911, significance level = 0.1%). Pairwise comparisons indicated that significant differences existed between all three dreissenid periods (Table 2).

Table 2. Results of analysis of similarities procedure testing for differences between dreissenid periods.

	Pairwise tests		
Groups	*R* statistic	Significance level	Permutations
Pre vs early	0.917	0.008	120
Pre vs late	0.994	0.001	792
Early vs late	0.754	0.018	56

Note: Pre, 1983–1990; early, 1991–1993; late, 1996–2000. Global R = 0.911. Significance level of sample statistic: 0.001.

Examination of the relative contributions of individual taxa to the dissimilarity between the different periods can help

Table 3. Average abundances (number·L^{-1}) by period (1983–1990, 1991–1993, and 1996–2000) and relative contribution to dissimilarity (δ) between different periods of individual taxa from spring phytoplankton communities in the eastern basin of Lake Erie.

(*a*) Comparison between predreissenid and lake postinvasion communities.

Species	1983–1990	1996–2000	δ_i	δ_i /SD(δ_i)	δ_i, %	$\Sigma\delta_i$, %
A. islandica	1 268	**59 691**	6.23	1.1	8.6	8.6
S. hantzschii	4 490	**46 003**	6.01	1.4	8.3	17.0
S. niagarae	**299 706**	909	5.88	1.1	8.2	25.1
Peridinium spp.	**105 663**	556	5.09	1.1	7.1	32.2
S. parvus	1 333	**23 336**	4.73	1.5	6.6	38.8
T. flocculosa	**79 276**	617	4.73	1.2	6.6	45.3
Gymnodinium spp.	**64 960**	325	4.07	1.3	5.7	51.0
Chrysophyte flagellates	**26 769**	15 791	2.72	1.3	3.8	54.7
Rhodomonas spp.	**22 714**	12 381	2.47	1.0	3.4	58.2
A. formosa	**31 653**	18	2.39	1.2	3.3	61.5
F. crotonensis	**41 086**	18	2.25	1.1	3.1	64.6
S. alpinus	**18 256**	6 003	2.23	1.4	3.1	67.7

(*b*) Comparison between predreissenid and early postinvasion communities.

Species	1983–1990	1991–1993	δ_i	δ_i/SD(δ_i)	δ_i, %	$\Sigma\delta_i$, %
A. islandica	1 268	**166 628**	6.82	2.1	11.6	11.6
S. niagarae	**299 706**	15 026	4.78	1.1	8.2	19.8
Peridinium spp.	**105 663**	17 808	4.41	1.2	7.5	27.3
T. flocculosa	**79 276**	7 219	3.8	1.2	6.5	33.8
Gymnodinium spp.	**64 960**	27 862	3.64	1.3	6.2	40.0
Chlamydomonas spp.	2 030	**31 824**	2.95	1.5	5.0	45.0
Chrysophyte flagellates	26 769	**127 564**	2.77	0.8	4.7	49.8
S. parvus	1 333	**16 132**	1.98	0.9	3.4	53.1
S. binderanus	12 370	**17 695**	1.83	1.3	3.1	56.3
Cryptomonas spp.	27 343	28 058	1.75	1.4	3.0	59.2
A. formosa	**31 653**	4 106	1.64	1.0	2.8	62.0
S. alpinus	**18 256**	5 692	1.64	1.2	2.8	64.8

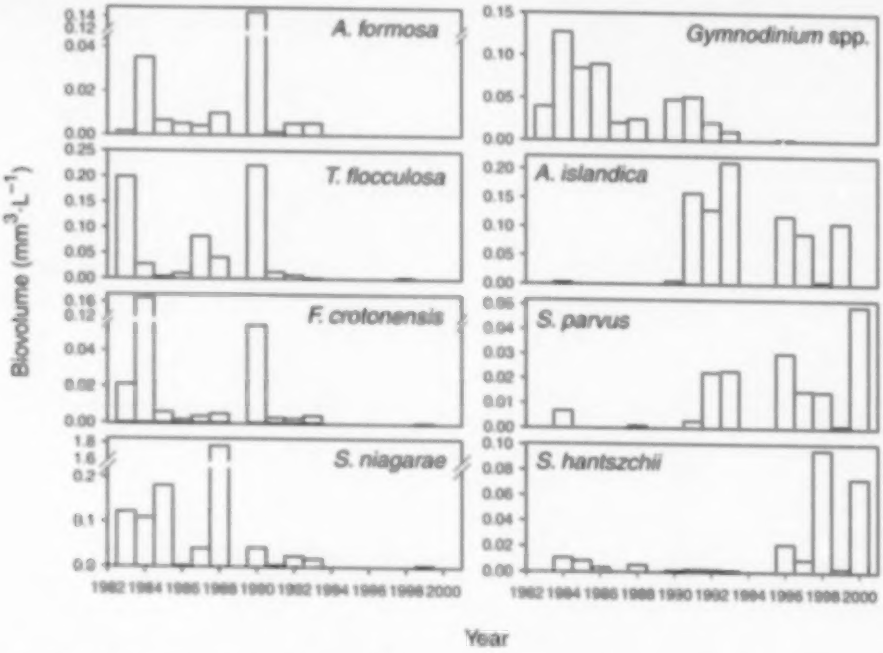
(*c*) Comparison between early and late postinvasion communities.

Species	1991–1993	1996–2000	δ_i	δ_i/SD(δ_i)	δ_i, %	$\Sigma\delta_i$, %
S. hantzschii	1 610	**46 003**	6.11	1.4	10.0	10.0
A. islandica	**166 628**	59 691	5.56	1.5	9.1	19.2
S. parvus	16 132	**23 336**	3.8	1.3	6.2	25.4
Chrysophyte flagellates	**127 564**	15 791	3.63	1.2	6.0	31.4
Chlamydomonas spp.	**31 824**	1 360	3.18	1.5	5.2	36.6
Gymnodinium spp.	**27 862**	325	2.96	0.9	4.9	41.4
Cryptomonas spp.	**28 058**	1 750	2.61	1.5	4.3	45.7
Rhodomonas spp.	**20 055**	12 381	2.3	1.1	3.8	49.5
S. binderanus	**17 695**	842	2.24	1.2	3.7	53.2
S. alpinus	5 692	6 003	2.12	1.1	3.5	56.7
Colonial cyanophytes	**11 221**	433	1.94	1.8	3.2	59.9
Picoplankton	**12 999**	1 174	1.84	1.4	3.0	62.9

Note: δ_i, contribution of species *i* to dissimilarity between period; SD(δ_i), standard deviation of δ_i; $\Sigma\delta_i$ (%), cumulative dissimilarity; for each comparison, the greater abundance is shown in bold.

identify the species most responsible for the shifts in community composition that have taken place. Only three species, all centric diatoms, contributed substantially to the dissimilarity between the pre-*Dreissena* and late postinvasion periods by their greater representation during the latter period (Table 3). These were *Stephanodiscus parvus*, the closely related *Stephanodiscus hantzschii*, and *Aulacoseira islandica*. A greater number of species contributed to the differences between these two periods by their relative absence during the later period. These included the pennate diatoms *Tabellaria flocculosa*, *Asterionella formosa*, and *Fragilaria crotonensis*, the centric diatoms *Stephanodiscus niagarae* and *Stephanodiscus alpinus*, and the pyrrophyte genera *Gymnodinium* and *Peridiniam*. Communities in the period immediately following the *Dreissena* invasion were distinguished from preinvasion communities by greater abundances of *A. islandica*, *S. parvus*, and *Stephanodiscus binderanus*, *Chlamydomonas*, and chrysophyte flagellates and by a relative lack of *S. niagarae*, *Peridinium*, *Gymnodinium*, *T. flocculosa*, *A. formosa*, and *S. alpinus*. The two postinvasion periods differed in the greater numbers of *S. hantzschii* and *S. parvus* during 1996–2000 and by the in-

Fig. 9. Average spring abundances of the dominant taxa in the eastern basin of Lake Erie, 1983–2000. Samples were not collected in 1989, 1994, or 1995.



creased populations of various flagellates and cyanophytes during 1991–1993. Although dominant during both postinvasion periods, the greater overall abundances of *A. islandica* in 1991–1993 also served to separate this period from the 1996–2000 postinvasion period.

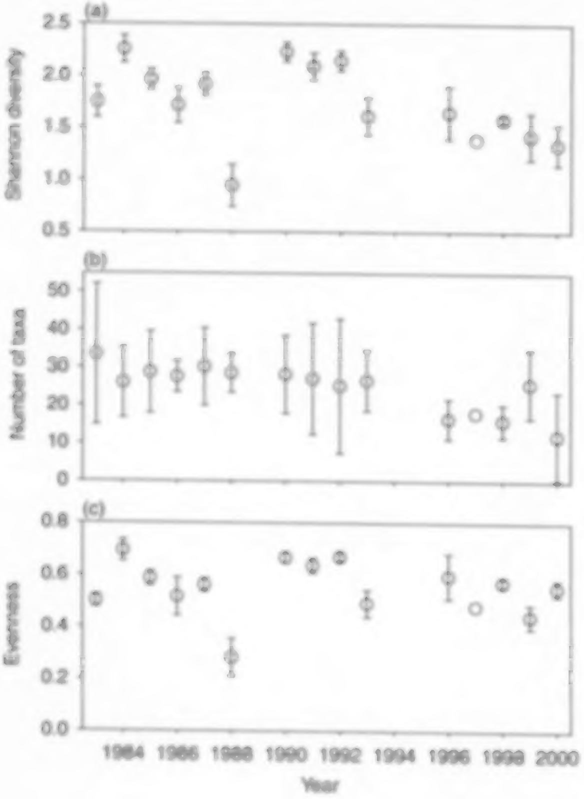
The picture that emerges is of a pre-*Dreissena* community dominated variously by a number of pennate diatoms species (*T. flocculosa*, *F. crotonensis*, *A. formosa*), the pyrrophytes *Peridinium* and *Gymnodinium*, and several larger *Stephanodiscus* species (*S. niagarae*, *S. alpinus*). In 1991, a change takes place, the most notable aspect of which is the appearance of *A. islandica*, although several "pre-*Dreissena*" species also persist through 1993. A further change is apparent by 1996, with overall biovolume substantially reduced, as noted above, and dominance restricted primarily to one or more of the three centric diatoms *A. islandica*, *S. parvus*, and *S. hantzschii*. Although present to an extent during the immediate postinvasion period, the pennate diatoms and pyrrophytes prevalent in the earlier communities all but disappear from the spring phytoplankton by 1996 (Fig. 9).

In addition to the reduction in overall phytoplankton community size and the shifts in community composition seen during the later postinvasion years, the species richness of later communities was statistically significantly lower than that of both pre-*Dreissena* and immediate postinvasion communities (Fig. 10; Table 4). This resulted in lower diversity in the later postinvasion communities compared with both the pre-*Dreissena* and early postinvasion communities. The dominant organisms in these later communities were drawn from a smaller number of species (i.e., *A. islandica*, *S. parvus*, and *S. hantzschii*) compared with both the pre-*Dreissena* communities and the immediate postinvasion communities, although this was offset by the overall lower number of species in 1996–2000, and thus there were no differences in evenness of the communities between the three periods.

Of the chemical variables measured in this study, changes in phytoplankton community composition, as measured by ordination axis scores, tracked most closely with alkalinity. A highly significant ($p < 0.001$, $r^2 = 0.65$) linear relationship was found between alkalinity and DCA axis 1 scores (Table 5; Fig. 11). As noted, we have interpreted alkalinity as an indication of dreissenid population increase, with the period of decreasing alkalinity (1991–1993) indicating a dreissenid community that was expanding sufficiently rapidly for calcium uptake by the mussels to exceed resupply from external inputs and regeneration from the sediments and the leveling off of alkalinity from 1996–2000 indicating a lessening of mussel population increase, with a consequent diminution in calcium uptake rate. It is important to note that changes in alkalinity would correspond to changes in the *rate* of dreissenid population increase, but not necessarily population size. A slowing in the rate of dreissenid expansion at a high population size could allow for the trend of decreasing alkalinity to reverse, depending on the rate of population turnover relative to external and internal inputs of calcium.

All three soluble nutrients were significantly correlated with DCA axis 1, as was Secchi depth, with silica showing the strongest correlation ($r = 0.763$; Table 6). Less pronounced, but still significant, correlations with axis 2 were found between total phosphorus and nitrate–nitrite nitrogen. Weighted average optima for the dominant species showed the expected pattern, i.e., generally higher soluble silica and phosphorus optima and tolerances for species associated with postinvasion communities (Fig. 12). Differences between pre- and post-invasion species were most notable for

Fig. 10. (*a*) Average spring diversity, (*b*) species richness, and (*c*) evenness of the phytoplankton community in the eastern basin of Lake Erie, 1983–2000. Bars represent ±1 SE.



silica optima, which ranged over an order of magnitude, from 0.88 mg $SiO_2 \cdot L^{-1}$ for *A. islandica* to 0.08 mg $SiO_2 \cdot L^{-1}$ for *A. formosa*.

Discussion

Following the introduction of *Dreissena*, distinct changes occurred in the size and composition of the spring phytoplankton community in the eastern basin of Lake Erie. By the mid-1990s, spring dominance had clearly shifted from a mix of pennate and large centric diatoms and pyrrophytes to the three centric diatoms *A. islandica*, *S. hantzschii*, and *S. parvus*, and both overall diversity and species richness of the spring phytoplankton community had declined significantly. In addition, total phytoplankton biovolume had decreased to approximately 20% of pre-*Dreissena* levels, whereas postinvasion concentrations of spring soluble nutrients, notably Si and TSP, were substantially elevated compared with earlier years. The coincident high nutrient concentrations and low biovolume seen during the postinvasion period strongly suggest that the spring phytoplankton community was being limited by grazing, rather than by nutrient supply, and the timing of these changes point to grazing by dreissenid mussels.

Table 4. Generalized linear model results testing for differences in richness, evenness, and Shannon–Wiener diversity between the three dreissenid periods (Dreis).

Source	*df*	Type III SS	Mean square	*F* value	*p*
Evenness					
Dreis	2	0.0624	0.0312	2.30	0.1071
Year(Dreis)	12	1.0344	0.0862	6.34	<0.0001
Diversity					
Dreis	2	1.868	0.9342	6.32	0.0028
Year(Dreis)	12	10.36	0.8634	5.84	<0.0001
Tukey's pairwise comparisons: pre early late					
Richness					
Dreis	2	1306.69	653.346	41.3	<0.0001
Year(Dreis)	12	655.20	54.600	3.45	0.0004
Tukey's pairwise comparisons: pre early late					

Note: Means joined by underscoring indicate no significant difference ($\alpha = 0.05$) as determined by pairwise tests using Tukey's honestly significance difference (HSD). Pre, 1983–1990; early, 1991–1993; late, 1996–2000.

There have been few previous field studies documenting unambiguous shifts in phytoplankton community makeup in systems invaded by dreissenids. Smith et al. (1998) reported a shift in taxonomic composition of phytoplankton assemblages, calculated on an annual average basis, from colonial and unicellular cyanobacteria to diatoms after the *Dreissena* invasion of the Hudson River. This was initially attributed to differential growth rates in the face of dreissenid grazing pressure. A subsequent laboratory study suggested that preferential ingestion of *Microcystis* could have accounted for the shift (Baker et al. 1998). The opposite was apparently found in Oneida Lake, New York, where significant decreases in summer and autumn diatom populations were seen after the dreissenid invasion, although this change was neither particularly marked nor permanent (Idrisi et al. 2001). In contrast to both reports above, Nicholls and Hopkins (1993) reported equally dramatic postdreissenid reductions in phytoplankton densities across all major taxonomic groups at a series of nearshore sites in Lake Erie. As with Smith et al. (1998), they based their analysis on average annual values. It is important to note that the main shifts that we have documented here, i.e., from pennate and some centric diatoms to other centric diatoms, took place within a major taxonomic group. This points to the importance of taxonomic resolution in determining the effects of invasive species on biological communities.

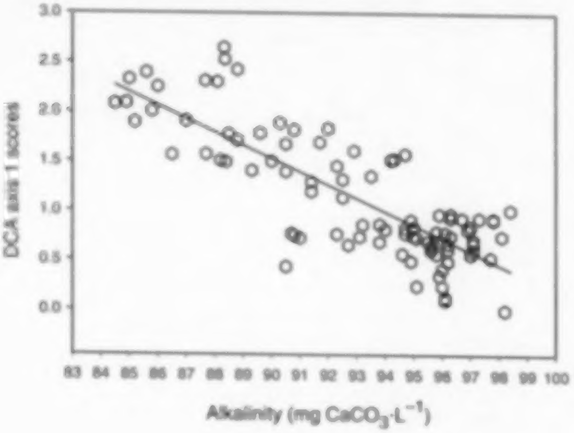
The changes in phytoplankton community composition seen in our study appear to be primarily the result of grazing-related reductions in nutrient demand. We believe that filtration by *Dreissena* spp. has reduced phytoplankton populations sufficiently to reduce silica uptake in the spring, and the resulting relaxation of silica limitation has shifted phytoplankton community structure towards a limited number of diatom species with high silica requirements. Kilham (1971) pointed out the importance of silica concentration in determin-

Table 5. Least squares regression and associated analysis of variance results for alkalinity (ALK) and detrended correspondence analysis axis 1 scores.

Predictor	Coefficient	Standard error	*t* ratio*	*p*	Source	df	SS	Mean square	*F* value	*p*
Intercept	13.6	0.961	14.14	<0.001	Regression	1	23.36	23.36	168.3	<0.001
ALK	–0.134	0.0103	–12.97	<0.001	Residual	89	12.35	0.139		
					Total	90	35.72			

*H_0: β = 0.

Fig. 11. Relationship between spring alkalinity and detrended correspondence analysis (DCA) axis 1 scores (see Fig. 7), as estimated by least squares regression.



ing the composition of diatom communities. The changes in diatom dominance that we have seen, particularly the shift from *A. formosa*, *T. flocculosa*, and *F. crotonensis* in predreissenid years to *A. islandica* and *S. hantzschii*, are consistent with a shift towards species associated with higher silica conditions, judging from patterns seen in the other Laurentian Great Lakes. In Lake Michigan, both *S. tenuis* (= *S. hantzschii*) and *A. islandica* are spring dominants that are replaced by *T. flocculosa*, *A. formosa*, and *F. crotonensis* as silica levels decline (Holland 1969; Parker et al. 1977; Fahnenstiel and Scavia 1987), and similar patterns have been seen in Lake Huron (Stevenson 1985) and Lake Ontario (Stoermer et al. 1974). The replacement of *A. formosa* and *F. crotonensis* with *A. islandica* is also consistent with calculated silica optima of these species in Lake Michigan (Barbiero et al. 2000). An improvement in the light climate, measured as Secchi depth, was also associated with the changes in the phytoplankton community, as indicated by the strong correlation between Secchi depth and the primary DCA axis. However, the preference of the main postdreissenid dominant, *A. islandica*, for low light environments is well documented (Lund 1954; Stoermer 1993), which suggests that the increase in light availability was more likely a consequence, rather than a cause, of the changes seen in the phytoplankton community. Within the postdreissenid community, the dominance of *S. hantzschii*, and the near complete absence of *A. islandica*, during 1998 and 2000 can probably be explained by the unusually high temperatures seen in these two years. While sharing many ecological characteristics, *S. hantzschii* has been shown to have a higher temperature optimum in the Great Lakes than *A. islandica* (Stoermer 1993).

Table 6. Results of Spearman rank correlations (*r*) between nitrate–nitrite nitrogen (NO$_3$), total phosphorus (TP), total soluble phosphorus (TSP), silica (Si), and Secchi depth (SD) and detrended correspondence analysis axis scores.

	NO$_3$	TP	TSP	Si	SD
Axis 1					
r	0.462	–0.105	0.466	0.763	0.746
p	<0.001	0.31	<0.001	<0.001	<0.001
n	95	95	95	95	25
Axis 2					
r	–0.253	–0.377	–0.163	–0.0494	0.047
p	0.013	<0.001	0.115	0.634	0.825
n	95	95	95	95	25

Because our data represent a narrow seasonal window, we cannot determine if the postinvasion dominants are appearing now for the first time, in response to the creation of a new niche space, or whether they were present before the alterations in nutrient regime but had population maxima earlier in the season, before substantial draw down of soluble silica. Apparent changes in species dominance could be due to such an alteration in the timing of succession, as a reduction in silica uptake could prolong the seasonal period of high silica concentration and thereby slow down the successional sequence. A graphical representation of this scenario is provided in Fig. 13. Based on the limited data available on predreissenid species succession in the eastern basin of Lake Erie, it is possible that the greater frequency of *S. hantzschii*, and perhaps also *S. parvus*, in our postinvasion samples is due to a change in the timing of their population development. It should be noted that *S. parvus* was first described in 1984 (and first identified in GLNPO samples from 1984) and would likely have been identified as the closely related *S. hantzschii* or *S. tenuis* in earlier reports, whereas *S. tenuis* has recently been determined to be a form of *S. hantzschii* (Håkansson and Stoermer 1984) and was treated as *S. hantzschii* in the present study. Munawar and Munawar (1976) reported a large population of *S. tenuis* in early April 1970, which was succeeded by a community of *Gymnodinium*, *Peridinium*, and *S. niagarae*, the latter corresponding closely to our predreissenid community. Nicholls (1981) also mentions spring pulses of *S. hantzschii* in samples taken in the late 1960s–1970s. It is possible, therefore, that the increased postinvasion populations of *S. hantzschii* that we have seen represent a shift in the timing of succession. However, recent comparisons of surficial sediments, which integrate diatom populations over the course of the

Fig. 12. Optima (points) and tolerances (vertical lines) for (*a*) silica and (*b*) soluble phosphorus, as determined by weighted averaging, for 16 most dominant taxa. Whiskers represent ±1 SE of optima estimates. Only diatom taxa are shown for silica.

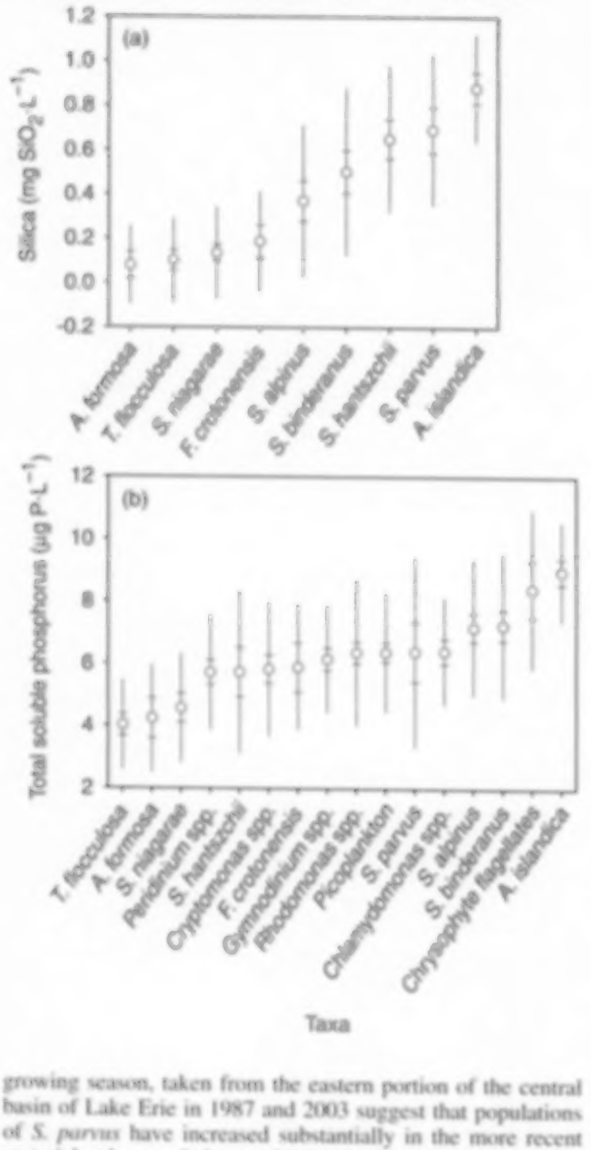
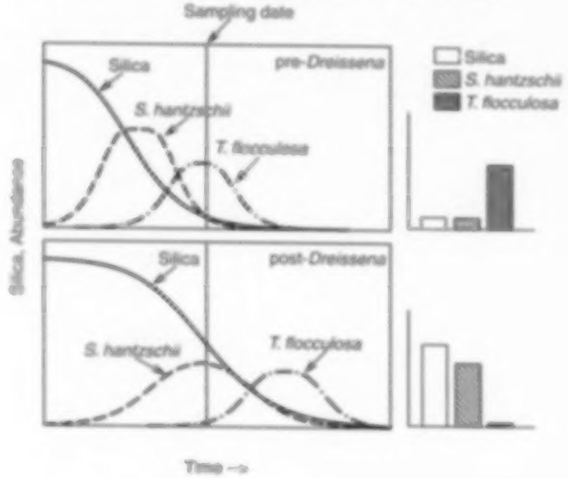


Fig. 13. Hypothetical time course of soluble silica concentration, population development of early successional (i.e., high silica) species (*Stephanodiscus hantzschii*) and later successional (i.e., low silica) species (*Tabellaria flocculosa*) before and after dreissenid invasion. Histograms on right indicate relative concentrations (or densities) of the three variables expected during the Great Lakes National Program Office's spring sampling for the two different scenarios, assuming constant sampling date.



growing season, taken from the eastern portion of the central basin of Lake Erie in 1987 and 2003 suggest that populations of *S. parvus* have increased substantially in the more recent material, whereas *S. hantzschii* has shown a modest increase (J. Wolin, Cleveland State University, 2121 Euclid Avenue, Cleveland, OH 44115, USA, personal communication). This suggests that large spring populations of *S. parvus* are a relatively recent phenomenon and do not represent merely a shift in timing of population maxima. This is probably also the case with the main postinvasion dominant *A. islandica*. Munawar and Munawar (1976) did not find *A. islandica* in substantial numbers in either the eastern or central basins in their seasonal study, and Stoermer et al. (1996) did not report finding *A. islandica* in an examination of a sediment core taken from the central basin of Lake Erie in the 1980s. *Aulacoseira islandica* was also rare in surficial sediments from the eastern central basin taken in 1987 but increased substantially by 2003. Conversely, *T. flocculosa*, which was an occasional spring dominant before the arrival of dreissenids, was virtually absent from the 2003 surficial sediments (J. Wolin, Cleveland State University, 2121 Euclid Avenue, Cleveland, OH 44115, USA, personal communication). Instead of a shift in the timing of dominance, therefore, *A. islandica* appears to be exploiting a new niche created by increased silica concentrations. The postinvasion increases in April silica concentrations are not only elevated in comparison to preinvasion concentrations during the same period, but also are well above previous seasonal maxima. Silica concentrations seen in April since the *Dreissena* invasion have averaged 0.76 mg $SiO_2 \cdot L^{-1}$, whereas winter maxima from our program in 1984 and 1985 were consistently below 0.32 mg $SiO_2 \cdot L^{-1}$. Similar (i.e., <0.4 mg $SiO_2 \cdot L^{-1}$) winter values have been reported from the 1960s and 1970s by Dobson et al. (1974) and Schelske et al. (1983).

One of the more dramatic impacts of the increases in anthropogenic nutrient loading on the Laurentian Great Lakes over the course of the last century has been the changes in silica dynamics brought about by eutrophication-related increases in phytoplankton productivity (Schelske et al. 2005). Schelske et al. (1986) have outlined four types of silica dynamics in the Great Lakes, each a consequence of progressively increasing levels of P enrichment. In their scheme, Lake Ontario and the central and eastern basins of Lake Erie exhibited the most extreme stage, where severe Si depletion occurs before thermal stratification and diatom populations are severely Si-limited during most of the year. The state of severe silica depletion found in the eastern basin of Lake Erie before the dreissenid invasion was a result of historical increases in P loading (Schelske et al. 1986). Sediment silica profiles in the eastern basin of Lake Erie show an increase in biogenic silica deposition in the late 19th century, presumably due to increased diatom productivity resulting from phosphorus loading from early settlement activities in the basin, with severe silica depletion occurring in the 1950s or 1960s (Schelske et al. 1983, 2005). Our data indicate that during most of the 1980s, silica concentrations had been reduced to extremely low levels by early to mid-April. After 1996, spring SiO_2 concentrations were on average more than triple preinvasion concentrations, exceeding 1.0 mg $SiO_2 \cdot L^{-1}$ in several years. As noted, not only spring concentrations of silica, but also the silica reservoir of the lake, have apparently increased since the dreissenid invasion, as would be predicted to result from the imposition of another source of limitation to diatom productivity (Schelske 1999). Such a situation has recently been seen in Lake Michigan, where reductions in phosphorus loading have resulted in a gradual recharge of the silica reservoir in that lake over the past 20 years (Barbiero et al. 2002). In the present case, limitation seems to have been brought about by grazing, although the effect is the same. Unlike Lake Michigan, however, the relatively short residence time of Lake Erie (2.7 years; Quinn 1992) and the relatively high silica concentrations in Lake Huron (Barbiero and Tuchman 2001), which is the main source of inflow for Lake Erie, should result in a rapid recharge of the silica reservoir of the lake (Schelske 1999), as in fact appears to be the case. Although the current increased silica content of the lake probably constitutes a state more similar to preindustrialization conditions, it does not necessarily follow that historic diatom assemblages will return. Paleolimnological work has shown that phosphorus abatement in Lake Erie has not resulted in the reestablishment of many previously abundant indigenous species, while some species that have increased since phosphorus controls have been implemented were not abundant in the preimpact flora (Stoermer et al. 1996).

We have assumed that the increased nutrient concentrations seen since the *Dreissena* invasion have been a consequence of reduced phytoplankton population growth rates and, therefore, uptake. However, dreissenids could theoretically also contribute more directly to increased soluble nutrient levels through excretion and (or) resolubilization. Numerous laboratory studies have suggested the ability of dreissenids to excrete substantial amounts of P and N (Heath et al. 1995; Arnott and Vanni 1996; James et al. 1997), and increases in soluble nutrients, specifically P and (or) N, after dreissenid colonization appear to be a common feature of affected systems (Holland et al. 1995; Effler et al. 1996; Caraco et al. 1997). Very little information is available on the effects of dreissenids on silica dynamics. In particular, there are no studies that we are aware of that document silica resolubilization by dreissenids, although grazing by zooplankton has been shown to facilitate redissolution by fragmenting frustules (Tessenow 1966). Holland et al. (1995) reported increases in Si, as well as N and P, in the western basin of Lake Erie immediately after dreissenid colonization. It is unclear to what extent these increases were due to silica resolubilization or to reduced demand from lower phytoplankton densities (Holland 1993). In perhaps the only other report to address changes in silica after a dreissenid invasion, Idrisi et al. (2001) found no change in soluble silica in Oneida Lake, New York.

In theory, dreissenid activities can also directly alter community makeup through selective removal and (or) ingestion or differential digestion of phytoplankton species. Dreissenid mussels can ingest particles up to 400 μm (Shevtsova et al. 1986), an upper limit that would likely include all of the species encountered in our study, but well-fed individuals have been shown to exhibit positive selection within the mantle cavity and (or) stomach for smaller (15–45 μm) particles (Ten Winkel and Davids 1982). Bastviken et al. (1998), however, did not find clear size-related changes in phytoplankton community composition in their short-term mesocosm experiments, and similarly Horgan and Mills (1997) found no relationship between particle size and dreissenid clearance rate in experiments using natural lake water from Oneida Lake, New York, which contained species of *Melosira* (= *Aulacoseira*). Likewise, it seems unlikely that size selectivity played a dominant role in restructuring the phytoplankton community in our study, as a number of large colonial diatoms exhibited dramatic, but contrasting, changes in density after the dreissenid invasion. Although the overwhelmingly dominant postdreissenid phytoplankter in our study, *A. islandica*, is a large-celled chain-forming diatom with morphology that could potentially present a challenge to ingestion by dreissenids, several other large colonial or chain-forming diatoms, e.g., *T. flocculosa*, *F. crotonensis*, and *A. formosa*, decreased in our study after the dreissenid invasion, which suggests that size selection was not the primary causative mechanism.

Dreissenids are known to be able to sort ingested material on the basis of factors other than size (Baker et al. 2000), although information on selectivity for specific phytoplankton species is sparse and often contradictory. Bastviken et al. (1998) found relatively low net clearance efficiencies of *Dreissena* for both *Aulacoseira* spp. and unicellular centric diatoms, which experienced increases in relative abundance in their short-term microcosm experiments. However, similar results were also found for *F. crotonensis*, a species that, as noted, declined in our study. Negative selection for diatoms was also found by Baker et al. (1998), who reported that the diatoms *Thalassiosira* and *Cyclotella* were generally excluded from ingestion and rejected as diffuse pseudofeces, which were easily resuspended. Lavrentyev et al. (1995), on the other hand, found that *Dreissena* selectively removed *Cyclotella*, as well as *Cryptomonas*, from 4 L containers but had no significant impact on *Microcystis*. Heath et al. (1995) found the greatest declines in diatoms and chlorophytes and relatively little impact on cyanophytes and chrysophytes in short-term enclosure experiments, whereas Wilson (2003) found minimal impacts by dreissenid mussels on phytoplankton community composition in long-term (5-week) field mesocosms, although diatoms constituted a relatively small proportion of the phytoplankton community in his study. The discrepancies seen between the various field and laboratory selectivity studies could in part be due to differences in the types of particles present in the water column. Baker et al. (1998) have shown that dreissenid selectivity of phytoplankton can differ depending on the exact makeup of the algal suspension offered, with some phytoplankters preferentially ingested if accompanied by some species but not by others. In any event, though, although selective filtration or ingestion might have been a contributing factor in promoting the species shifts seen in our study, there seems to be limited evidence to support selectivity as the main mechanism.

This study has documented for the first time clear and sustained species-level shifts in a phytoplankton community following an invasion by dreissenid mussels. These shifts are associated with both a dramatic reduction in phytoplankton biovolume and a marked increase in soluble silica concentration, which taken together suggest a strongly grazing-impacted community. Given the timing of these changes, we believe that filtration by *Dreissena* spp. is responsible for the reduced phytoplankton populations, and the consequent relaxation of silica limitation has shifted phytoplankton species composition towards diatoms with high silica requirements. Although the association in our data between species composition and silica is strong, we cannot rule out the possibility that selective filtration by dreissenids has also contributed to the species shifts seen. The apparent limitation of phytoplankton, particularly diatom, growth by dreissenid filtration has not only slowed silica uptake in spring, but also seems to have lead to an increase in the overall silica content of the eastern basin of Lake Erie, thus fundamentally altering silica dynamics in this basin of the lake.

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A hierarchical model for salmon run reconstruction and application to the Bristol Bay sockeye salmon (*Oncorhynchus nerka*) fishery

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Abstract: The goal of spreading the annual catch of a Pacific salmon (*Oncorhynchus* spp.) run proportionally across all segments of the migration is rendered difficult or impossible because of the interannual variability in both run size and run timing. This problem is particularly acute in the case of the fishery for sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay, Alaska, for which traditional run reconstruction models are not applicable because of the extreme temporal compression of the run. We develop a run reconstruction model appropriate for sockeye salmon in Bristol Bay by accounting for the hierarchical structure of the problem and by including process error. Our results indicate that the hierarchical structure is, in fact, not necessary, whereas the process error parameters are needed to fit the data. We suggest further model development without the hierarchical structure, including incorporating in-river test fishing data. The results of our method can be used to address questions regarding environmental or intrinsic drivers of run timing and the possibility of artificial selection on run timing.

Résumé : L'objectif de répartir les prises annuelles d'une montaison de saumons du Pacifique (*Oncorhynchus* spp.) de façon proportionnelle dans tous les secteurs de la migration devient difficile ou impossible à atteindre à cause de la variabilité d'une année à l'autre de l'importance et du calendrier de la montaison. Le problème est particulièrement difficile dans le cas de la pêche de saumons rouges (*Oncorhynchus nerka*) de la baie de Bristol, Alaska, pour laquelle les modèles courants de reconstruction de la montaison ne sont pas utilisables à cause de l'extrême compression temporelle de cette montaison. Nous mettons au point un modèle de reconstruction de la montaison approprié aux saumons rouges de la baie de Bristol, en tenant compte de la structure hiérarchique du problème et en introduisant l'erreur de processus. Nos résultats indiquent que la structure hiérarchique n'est, en fait, pas nécessaire, alors que les paramètres de l'erreur de processus est requise pour l'ajustement des données. Nous suggérons que le modèle soit développé sans la structure hiérarchique, mais en incorporant des données de pêche expérimentale dans la rivière. Notre méthodologie peut servir à étudier des questions concernant les variables environnementales ou intrinsèques qui contrôlent le calendrier de la montaison et la possibilité de faire une sélection artificielle dans le calendrier de la montaison.

[Traduit par la Rédaction]

Introduction

Populations of Pacific salmon (*Oncorhynchus* spp.) have evolved mechanisms to synchronize spawning dates in accordance with local temperature regimes (Brannon 1987). "Simply put, the adults spawn at a date that, given the average thermal regime, will allow the embryos to complete embryonic development and emerge in time to feed on aquatic insects and zooplankton the following spring" (Hilborn et al. 2003, p. 6564). Fisheries on a particular "run" often target a complex of stocks, with spawn timing (among other life-history traits) for each stock adapted to different local environments within a watershed (e.g., Rogers 1987) or collection of watersheds (e.g., Hilborn et al. 2003). The standard management policy for commercial salmon fisheries in Alaska is to spread an annual target catch proportional to run strength across all segments of the migration to better ensure the escapement (fish passing through the commercial fishing district that are assumed to spawn) of spawners from each time segment and thus avoid artificial selection on run timing (Mundy 1982).

Managers of Pacific salmon fisheries have to ensure that escapements are within a target range and that catches are proportional to run strength. However, escapement counts often can not be made until the migrating salmon are no longer vulnerable to harvest. For example, in the case of the sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay (Fig. 1), escapement counts can not be made until the fish have passed the fishery and reached areas with sufficiently clear water for counting towers to operate. Therefore, managers must make decisions to open or close the fishery before reliable estimates of escapement are available. Early indices of the number of fish available for catch or spawning escapement typically come from estimates of (*i*) the number of fish that have passed through the fishery that have not yet reached the escapement counting areas, (*ii*) the number of fish in the commercial fishing district, and (*iii*) some esti-

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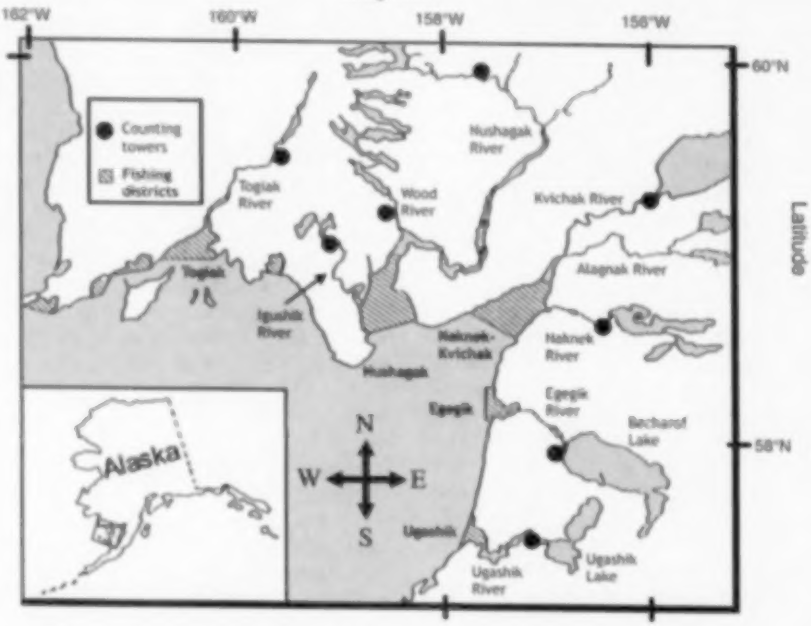
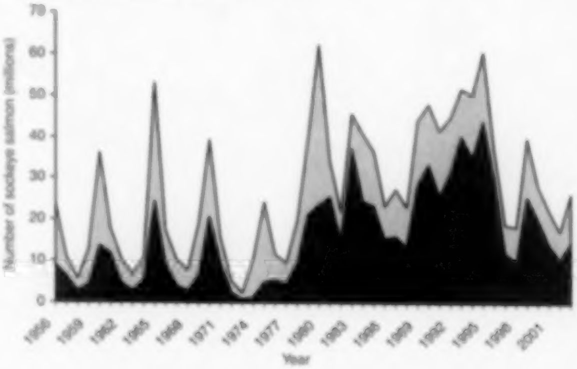
Fig. 1. Commercial fishing districts and counting towers for sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay, Alaska (adapted from Minard and Meacham (1987, p. 336)).



mate of the strength of the run not yet present in the fishing district, provided by an intercept fishery or a directed test fishery.

Estimating in-season run strength would be relatively simple if run timing were the same each year, because management biologists, knowing the number of fish that have arrived by a given date and the corresponding historical average proportion of the run, would need only to perform a simple calculation to predict run size. However, in many salmon fisheries, early indicators of run strength are completely confounded by variability in run timing, and vice versa. For example, a large showing of fish early in the season may indicate a large run and (or) an early run; the actual combination of run size and run timing will be indistinguishable until a possibly substantial portion of the run is beyond the fishery. The one Pacific salmon species for which this problem has been addressed satisfactorily is pink salmon (*Oncorhynchus gorbuscha*). Male pink salmon return slightly earlier on average than female pink salmon, so the sex ratio of early catches indicates how much of the run has progressed (Zheng and Mathisen 1998). Unfortunately, all other species of Pacific salmon display variability in age-at-maturity, resulting in multiple size classes of fish (i.e., see Flynn and Hilborn 2004) and hence difficulty in interpreting sex ratio data (Zheng and Mathisen 1998).

Fig. 2. Historical runs (escapements + catches; shaded area) and catches (solid area) of sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay, Alaska, 1956–2003.



The Bristol Bay, Alaska, sockeye salmon fishery

The fishery for sockeye salmon in Bristol Bay, Alaska (Fig. 1), presents a unique challenge. In common with Pacific salmon targeted in other fisheries, the harvest of Bristol Bay sockeye has varied substantially over time, with the harvest ranging from less than one million to more than 44 million fish since 1956 (Fig. 2). Moreover, the run is temporally compressed, with roughly 80% of the harvest occurring between 27 June and 12 July (Helton 1991). If the run is much larger than expected, processors are not able to increase processing capacity quickly and may be forced to institute catch limits or ship unprocessed fish to distant plants with concomitant increased costs and decreased quality. Conversely, if runs are smaller than expected and there is excess capacity, the associated fixed costs may reduce profitability substantially. Furthermore, the amount of uncertainty is particularly great for Bristol Bay sockeye salmon because the run is so temporally compressed. In fact, a change of only 1 or 2 days in run timing can affect the appearance of the incoming run by millions of fish (Lowell Fair, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518, USA, personal communication).

Bristol Bay sockeye salmon return to a collection of river systems grouped into five commercial fishing districts (Togiak, Nushagak, Naknek-Kvichak, Egegik, and Ugashik; Fig. 1). Fish migrate into the bay through the commercial fishing districts and most of the distance upriver from the fishing districts to their rearing lakes before passing the Alaska Department of Fish and Game counting towers where they are counted as "escapement". The Togiak district typically constitutes only approximately 1%–3% of the total Bristol Bay commercial catch and is therefore excluded from this analysis. The Nushagak district is comprised of three major river systems, the Wood River, the Nushagak River, and the Igushik River. The Naknek–Kvichak district is also comprised of three major systems, the Kvichak River, the Naknek River, and the Alagnak River. The Egegik and the Ugashik districts are each comprised of only one river system, the Egegik and Ugashik rivers, respectively. Although there is evidence of stock structure within river systems (Rogers 1987; Hilborn et al. 2003), it is not logistically possible to manage at the subriver level, and thus "river" is equivalent to "population" for our purposes. Although each river is managed independently with its own escapement goal, commercial fishing in a district targets fish returning to all of its component rivers simultaneously. Determining the stock composition of daily commercial catches (via scale pattern analysis, genetic markers, etc.) is not presently possible in a timely or economical manner. Finally, although the timing of return migrations to the various river systems overlaps to a great degree, they are not identical.

Although preseason run-size forecasts for sockeye salmon in Bristol Bay are available and provide some indication of eventual run strength (i.e., Hyun et al. 2005), these preseason estimates need to be adjusted in-season as indicators of actual run size emerge (Fried and Hilborn 1988). A reliable method of forecasting run timing would enable Bristol Bay management biologists to estimate total run sizes more reliably in-season. This would, in turn, allow them to better set fishery openings to ensure that harvest rates are constant throughout the duration of the run while escapements remain within their target ranges. In this paper, we concentrate on estimating annual mean run timing parameters, both to gain an understanding of how timing varies interannually and to lay the groundwork for later attempts to predict run timing using environmental variables (i.e., sea surface temperatures) or characteristics of the run itself (i.e., age composition).

Salmonid run reconstruction models

Two primary methods have been used to calculate run timing in Bristol Bay: (*i*) the Alaska Department of Fish and Game (ADF&G) method and (*ii*) the Don Rogers' method. However, each method ignores one or more aspects of migration dynamics, which may result in inaccurate or even biased estimates of the runs' timing.

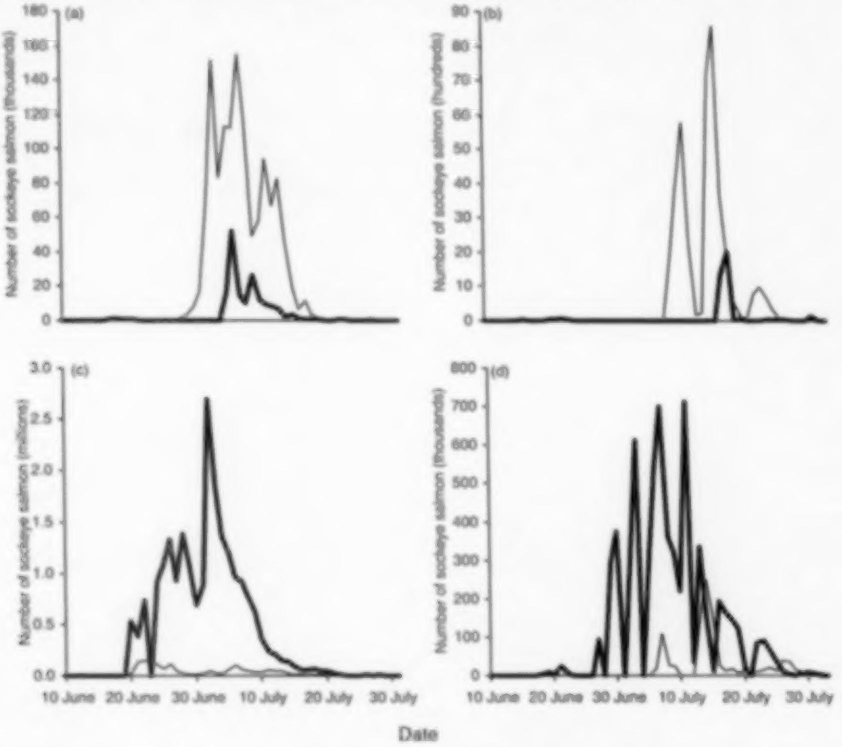
The ADF&G has traditionally defined the median run date as the date of 50% of "catches plus escapements to date". This method ignores the time spent pooling in the commercial fishing districts and the time spent traveling upriver between the fishing districts and the escapement counting towers and may be substantially biased because large runs are subject to higher harvest rates, so a larger proportion of the fish are counted in the fishing district (i.e., see Fig. 3). The fish caught in the commercial fishery will be counted as arriving earlier than the same fish if it passed through to the counting tower.

Don Rogers (University of Washington, School of Aquatic and Fishery Sciences, P.O. Box 355020, Seattle, WA 98195, USA, unpublished data) defined an index of run timing for each river by subtracting a "lag time" between the fishing district and the escapement count from the escapement dates. This lag time was determined by visually examining plots of catch and escapement by date for each Bristol Bay river system, identifying the most clear "valleys" in catch followed by "peaks" in escapement (i.e., see Fig. 3), and declaring the intervening time interval (an integer number of days; constant within each season) to be the lag time for that river in that year. The estimated lag times ranged from 3 to 9 days for the Egegik River and from 5 to 11 days for the Ugashik River. Although the Rogers' median run date method accounts for the geographic discrepancy in the two points of intercept, it is highly subjective.

Formal run reconstruction (or run timing) models can be applied to estimate run timing. For example, Schnute and Sibert (1983) developed a run timing model for use with terminal fisheries. This model consisted of five main components: (*i*) a bell-shaped curve that describes the rate at which salmon enter the fishery, (*ii*) the process by which fish accumulate in a fishery pool and are exposed to capture, (*iii*) a time lag between the fishery and a hatchery, (*iv*) a test fishery, and (*v*) an error term. Schnute and Sibert (1983) took the estimate of the mean of the bell-shaped curve as an index of run timing. Unfortunately, this method seems inappropriate for Bristol Bay sockeye salmon because arrivals to the various commercial fishing districts do not appear to conform to any known parametric distribution, but are characterized by sharp peaks and valleys (e.g., Fig. 3). This may be due to the relatively contracted nature of the runs compared with other salmon fisheries, or because the underlying distribution may be disguised considerably by some other influence such as tidal processes, fluctuations in river flow, or wind patterns.

Starr and Hilborn (1988) developed a model for use in situations in which multiple stocks travel through gauntlet fisheries enroute to more than one terminal fishery. Escapement data and travel times through the fishery areas are used to back-calculate the number of fish available for harvest in each gauntlet fishery during each time period during the season. Starr and Hilborn (1988) assumed known migration paths through each area and known, deterministic, pooling times in each area. Cave and Gazey (1994) converted this model from a backwards run reconstruction model into a forwards "preseason planning" model. Whereas the run reconstruction model estimates harvest rates and arrivals given catches, escapements, and assumptions about the rate of movement of fish, the preseason planning model calculates catch and escapement from assumed harvest rates, an assumed (normal) arrival pattern, and assumptions about fish movement. Templin et al. (1996) extended the model developed by Starr and Hilborn (1988) to allow for stochastic migration using a transition

Fig. 3. Catches (thick lines) and escapements (thin lines) by date for (*a* and *b*) the smallest (Egegik (1974) and Ugashik (1973), respectively) and (*c* and *d*) the largest (Egegik (1993) and Ugashik (1985), respectively) runs. Note the differing *y* axes; Egegik's 1974 escapement was greater in 1993 than in 1974 (approximately 1.1 million sockeye salmon, *Oncorhynchus nerka*, in *a* versus 1.5 million in *c*), and Ugashik's escapement was greater in 1985 than in 1973 (approximately 0.4 million in *b* versus 1.0 million in *d*). For comparison with subsequent figures, 10 June corresponds to Julian date 161, and 30 July corresponds to Julian date 212.



matrix, the parameters of which were estimated from the results of an earlier tagging study (Templin (1995), as cited in Templin et al. (1996)).

Although the models developed by Starr and Hilborn (1988), Cave and Gazey (1994), and Templin et al. (1996) allow for nonparametric distributions of arrival density, they assume constant, deterministic, pooling, and (or) travel time parameters. In contrast, Don Rogers' annual lag time estimates over the period of 1969–2003 ranged from 3 to 9 and from 5 to 11 days for Egegik and Ugashik, respectively, and Hodgson (2000) found evidence that river flow and river temperature may affect these travel times, both in Bristol Bay and in other Pacific sockeye salmon systems.

In this paper, we develop a run reconstruction model to work within the constraints imposed by the fishery for sockeye salmon in Bristol Bay and estimate indices of run timing at the river system level. Arrival to the commercial fishing districts is assumed to conform to a normal distribution, modified by process error to account for arrival patterns that do not conform exactly to a parametric distribution. Pooling times are modeled separately for the district and for the river because fish pooling in the commercial fishing district can "build up" over a period of days until an extremely large number of fish are vulnerable to harvest, whereas in the river, the pooling times describe the period required to migrate from the fishing district to the counting tower. We limit our analysis to the single-river systems of Egegik and Ugashik. Although the method can be extended straightforwardly to handle the three-river system, this is both computationally and presentationally complex.

Materials and methods

Data compilation

Historical daily catches by commercial fishing district and escapements by river system were provided by Lowell Fair of the Alaska Department of Fish and Game (333 Raspberry Road, Anchorage, AK 99518, USA). Escapement data were collected by counting towers throughout the data series. Each river has one counting tower on each side, and fish passing each tower are enumerated for 10 min out of each hour, with these counts expanded to the entire hour. (It is assumed that all fish travel up one side of the river or the other along the bank, and aerial surveys repeatedly justify this assumption.) Catch data are calculated by repeatedly sampling district commercial catches for average weights throughout the season and extrapolating. We assumed that the catches were known without error, whereas the escapements are subject to measurement error. Implicit in the former assumption is that all reported catches comprise fish enroute to the river in question and that all such fish were either caught or escaped, i.e., we ignored the possibility of interception. Catches were not reported daily before 1969, but rather were averaged over several days, so the analysis was limited to the years 1969–2003.

Model

The model of the dynamics of the population is outlined for clarity (Fig. 4), and the mathematical symbols used to construct the model are detailed in Appendix A.

The population dynamics model

Because fish arrival to the commercial fishing district does not follow any known parametric distribution exactly, we chose to adapt the previously used normal distribution of arrival density in time (Schnute and Sibert 1983) to include log-normally distributed process error. The number of fish arriving on day i of year y, $A_{i,y}$ is calculated as

$$(1)\qquad A_{i,y} = S_y \frac{\exp\left(-\frac{(i-\mu_y)^2}{2\sigma_y^2} + P_{i,y}\right)}{\sum_i \exp\left(-\frac{(i-\mu_y)^2}{2\sigma_y^2} + P_{i,y}\right)}$$

where μ_y is the mean date of arrival in year y assuming no process error, σ_y is the standard deviation of the date of arrival in year y before accounting for process error, S_y is the total run size for year y (the sum of the catches and escapements), and $\mathbf{P}$ is a matrix of normally distributed random variable with standard deviation σ_P.

Fish that arrive in the commercial fishing district on day i of year y are assigned to the diagonal $D_{i,i,y}$ of the matrix $\mathbf{D}$, the matrix that determines the number of fish arriving on day i, present on day j, of year y. They pool in the commercial fishing district for some period of time, during which they are vulnerable to harvest, and leave either by being caught or by migrating into freshwater. The number of fish that arrived in the fishing district on day i of year y that are still be there on day $j + 1$ of year y, $D_{i,j+1,y}$, is

$$(2)\qquad D_{i,j+1,y} = D_{i,i,y}\prod_{d=i}^{j}(1-h_{d,y})(1-m_{d-i,i,y})$$

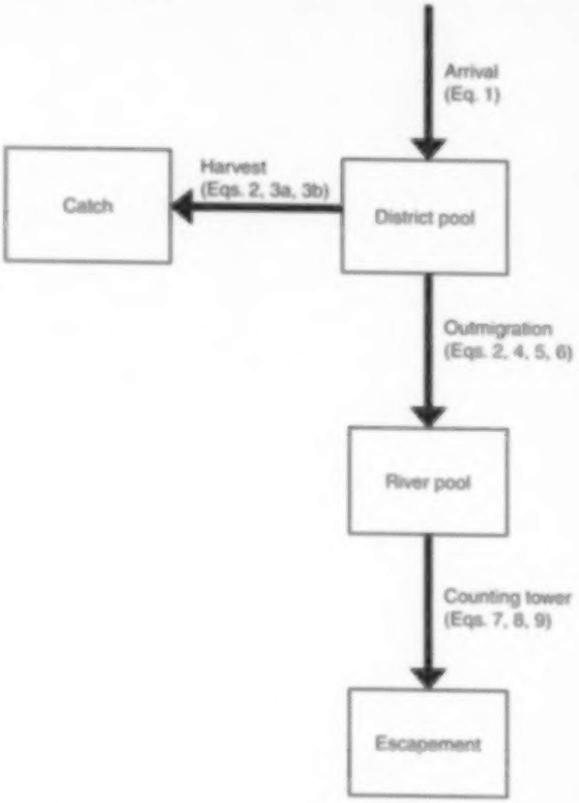
where $h_{j,y}$ is the harvest rate on day j of year y, and $m_{x,i,y}$ is the proportion of fish that arrived on day i of year y that outmigrate x days after arriving in the district (see eq. 5). The value of $h_{j,y}$ is calculated in two steps. The "raw" harvest rate on day j of year y is calculated as

$$(3a)\qquad h_{j,y}^{*} = \frac{C_{j,y}}{\sum_i D_{i,j,y}}$$

where $C_{j,y}$ is the actual catch of fish on day j of year y. This harvest rate is adjusted so that it cannot exceed 100%:

$$(3b)\qquad h_{j,y} = \frac{(h_{j,y}^{*} + K_H)^{\alpha}}{\beta + (h_{j,y}^{*} + K_H)^{\alpha}}$$

Fig. 4. Model flow diagram showing equations used to transition between each stage.



Equation 3b has the desirable property that it is both continuous and a differentiable function of the parameters of the model. The values selected for α and β (2.8168 and 0.11013, respectively) were chosen so that $h_{j,y}$ mimics $h_{j,y}^{*}$ closely when $h_{j,y}^{*} < 1.0$ and is close to 1.0 when $h_{j,y}^{*} > 1.0$. The constant K_H was created simply to ensure numerical stability when $h_{j,y} = 0$ and was set to 1.0×10^{-10}.

Residence time in the commercial fishing district was assumed to be normally distributed. The outmigration probabilities were therefore calculated from a truncated normal distribution with mean $\lambda_{i,y}$ and standard deviation of σ_λ. The parameter $\lambda_{i,y}$, the mean number of days (before truncation) spent in the commercial fishing district by fish arriving on day i of year y, is believed to decrease as the run progresses (Lowell Fair, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518, USA, personal communication). This is modeled by assuming that the mean travel time up the river changes (typically decreases) linearly throughout the season and $\lambda_{i,y}$ is therefore calculated using the equation

$$(4)\qquad \lambda_{i,y} = \lambda_{f,y} + \left(\frac{\lambda_{f,y} - \lambda_{l,y}}{l-f}\right)(i-f)$$

where $\lambda_{f,y}$ is the mean number of days spent in the commercial fishing district by fish arriving on the first day considered in the model (day f) during year y, and $\lambda_{l,y}$ is the mean number of days spent in the river by fish entering the river on the last day considered in the model (day l). Day f was set to Julian date 161 (10 June) for the Egegik and Ugashik rivers. Day l was set to Julian date 212 (31 July) for the Egegik River and to Julian date 215 (3 August) for the Ugashik River. Different last dates are considered for the two rivers because sockeye salmon in the Ugashik River tend to run slightly later than those in the Egegik River. Note that Julian dates are used throughout the rest of the paper.

The value of $m_{x,i,y}$, the proportion of fish arriving on day i of year y, entering the river after spending x days in the commercial fishing district, is determined using the equation

$$(5)\qquad m_{x,i,y} = \begin{cases} 1 - \displaystyle\sum_{z=x+1}^{x_{\max}} m^{*}_{z,i,y} \left(\sum_{z'=x}^{x_{\max}} m^{*}_{z',i,y} \right)^{-1} & \text{if } x < x_{\max} \\ 1 & \text{otherwise} \end{cases}$$

where

$$m^{*}_{x,i,y} = \frac{\exp\left(-\dfrac{(x-\lambda_{i,y})^2}{2\sigma_\lambda^2} \right)}{\displaystyle\sum_{z=x_{\min}}^{x_{\max}} \exp\left(-\dfrac{(z-\lambda_{i,y})^2}{2\sigma_\lambda^2} \right)}$$

Setting σ_λ to 0.5 resulted in ~10% of the fish spending one less day than the mean residence time for fish arriving on that day, ~80% spending the mean number of days of residence time there, and ~10% spending one more day than the mean residence time there. The value of $x_{\min}$ is set to 1 day, and $x_{\max}$ is set to 15 days, although $m^{*}_{x,i,y}$ is 1.0 well before day 15 in most cases.

The catch is (arbitrarily) removed before migration, so the number of fish that were present in the river at the start of day j of year y that outmigrated that day is

$$(6)\qquad R_{j,j,y} = \sum_i D_{i,j-1,y}(1-h_{j-1,y})m_{j-i,i,y}$$

where $R_{i,j,y}$ is the number of fish that entered the river on day i of year y and are still present in the river on day j of year y.

The approach used to model migration up the river is the same as that used to model pooling in the fishing district, except that no account needs to be taken of harvest. The number of fish entering the river on day j, still present on day k of year y that will still be present on day $k + 1$ of year y, is calculated as

$$(7)\qquad R_{j,k+1,y} = R_{j,k,y}(1-n_{k-j})$$

where n_w is the probability of migrating out of the river pool (i.e., passing the counting tower) for fish that have spent w days in the river, i.e., $k - j$ days. The variable n, unlike m, is not day- or year-specific. ADF&G has developed estimates of in-river travel time that they believe to be relatively constant both between and within seasons (Lowell Fair, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518, USA, personal communication).

The value of n_w is calculated using the equation

$$(8)\qquad n_w = \begin{cases} 1 - \displaystyle\sum_{z=w+1}^{w_{\max}} n^{*}_{z} \left(\sum_{z'=w}^{w_{\max}} n^{*}_{z'} \right)^{-1} & \text{if } w < w_{\max} \\ 1 & \text{otherwise} \end{cases}$$

where

$$n^{*}_{w} = \frac{\exp\left(\dfrac{(w-\theta)^2}{2\sigma_\theta^2} \right)}{\displaystyle\sum_{z=w_{\min}}^{w_{\max}} \exp\left(\dfrac{(z-\theta)^2}{2\sigma_\theta^2} \right)}$$

θ is the mean number of days (before truncation) spent in the river, and the standard deviation σ_θ determines the variability associated with the number of days spent in the river. σ_θ, the in-river pooling time, is also assumed to be 0.5, as ADF&G is confident in their estimates of θ. The minimum number of days spent pooling in the river, $w_{\min}$, was set to 1. The maximum number of days spent pooling, $w_{\max}$, was set to 5, as the relatively small standard deviation of 0.5 ensures that almost all fish will pool between 2 and 4 days in Egegik River and between 3 and 5 days in Ugashik River.

The model estimate of the number of fish moving out of the river pool (passing the counting tower) on day $k + 1$ of year y is

$$(9)\qquad \hat{T}_{k+1,y} = \sum_j (R_{j,k,y}\, n_{k-j})$$

The medians of the vectors $A_y = \{A_{f,y},\ldots,A_{l,y}\}$ are used to calculate the "run reconstruction median return date" for each year.

The objective function

The values for the parameters of the model (Table 1) are estimated by minimizing an objective function that consists of seven components: (*i*) the likelihood of the observed escapements (the tower counts), (*ii*) a penalty on the deviation of the vector $\boldsymbol{\mu} = \{\mu_{1980},\ldots,\mu_{2003}\}$ from a hyper-mean, (*iii*) a penalty related to the prior probability of χ, (*iv*) a penalty related to the prior probability of the hyper-standard deviation of the vector $\boldsymbol{\mu}$, ρ, (*v*) a penalty for the deviation of the matrix of process error parameters, $\mathbf{P} = \{P_{f,1980},\ldots,P_{l,2003}\}$, from zero, (*vi*) a penalty for the deviation of the vector of mean district residence time parameters from Julian date 185 (approximately at the midpoint of the run), and (*vii*) a penalty for harvesting more fish than are estimated to be available in the district on any given day. Each of these terms is outlined below.

The likelihood of the observed escapements is

$$(10)\qquad L(\cdot|\boldsymbol{\mu},\boldsymbol{\sigma},\cdot,\boldsymbol{\lambda}_f,\boldsymbol{\lambda}_l,\boldsymbol{\sigma}_T) = \prod_y \prod_k \frac{1}{\sqrt{2\pi}\,(\sigma_{T,y}\,T_{k,y}+K_T)} \times \exp\left(-\frac{(\hat{T}_{k,y}-T_{k,y})^2}{2(\sigma_{T,y}\,T_{k,y}+K_T)^2} \right)$$

The standard deviation of the difference between the expected and observed tower counts is calculated as $\sigma_{T,y}\,T_{k,y} + K_T$, where K_T is set to 0.1 and $\sigma_{T,y}$ is an estimated parameter. K_T is included in the standard deviation so that small tower counts are not overweighted relative to large tower counts.

Table 1. The parameters of the model and how their values are determined.

	Symbol	No hyper-priors	With hyper-priors		
Category	σ_ρ	0.5	0	0.3	0.5
(*a*) Egegik					
Parameters	μ_y	Estimated (35)	Estimated (35)	Estimated (35)	Estimated (35)
	ρ	N/A	Estimated (1)	Estimated (1)	Estimated (1)
	χ	N/A	Estimated (1)	Estimated (1)	Estimated (1)
	σ_y	Estimated (35)	Estimated (35)	Estimated (35)	Estimated (35)
	$P_{t,y}$	Estimated (1820)	0	Estimated (1820)	Estimated (1820)
	$\lambda_{f,y}$	Estimated (35)	Estimated (35)	Estimated (35)	Estimated (35)
	$\lambda_{l,y}$	Estimated (35)	Estimated (35)	Estimated (35)	Estimated (35)
	σ_λ	0.5	0.5	0.5	0.5
	θ	2	2	2	2
	σ_θ	0.5	0.5	0.5	0.5
	σ_F	Estimated (35)	Estimated (35)	Estimated (35)	Estimated (35)
Penalty terms	ψ	N/A	184	184	184
	ξ	N/A	20	20	20
	ν	N/A	7	7	7
	s^2	N/A	9	9	9
	$\mu_{\lambda_{\mathrm{ser}}}$	3.6	3.6	3.6	3.6
	$\sigma_{\lambda_{\mathrm{ser}}}$	1.6	1.6	1.6	1.6
	σ_ν	0.5	0.5	0.5	0.5
Total estimated		1995	177	1997	1997
(*b*) Ugashik					
Parameters	μ_y	Estimated (35)	Estimated (35)	Estimated (35)	Estimated (35)
	ρ	N/A	Estimated (1)	Estimated (1)	Estimated (1)
	χ	N/A	Estimated (1)	Estimated (1)	Estimated (1)
	σ_y	Estimated (35)	Estimated (35)	Estimated (1925)	Estimated (35)
	$P_{t,y}$	Estimated (1925)	0	Estimated (1925)	Estimated (1925)
	$\lambda_{f,y}$	Estimated (35)	Estimated (35)	Estimated (35)	Estimated (35)
	$\lambda_{l,y}$	Estimated (35)	Estimated (35)	Estimated (35)	Estimated (35)
	σ_λ	0.5	0.5	0.5	0.5
	θ	3	3	3	3
	σ_θ	0.5	0.5	0.5	0.5
	σ_F	Estimated (35)	Estimated (35)	Estimated (35)	Estimated (35)
Penalty terms	ψ	N/A	190	190	190
	ξ	N/A	20	20	20
	ν	N/A	7	7	7
	s^2	N/A	9	9	9
	$\mu_{\lambda_{\mathrm{ser}}}$	4.6	4.6	4.6	4.6
	$\sigma_{\lambda_{\mathrm{ser}}}$	1.3	1.3	1.3	1.3
	σ_ν	0.5	0.5	0.5	0.5
Total estimated		2100	177	2102	2102

Note: The values in parentheses indicate the number of parameters of each type.

The penalty for the deviation of the vector of mean run timing parameters, $\boldsymbol{\mu}$, from the hyper-mean run timing parameter, χ, is assumed to be normally distributed:

$$(11)\quad L(\boldsymbol{\mu}\,|\,\chi,\rho) = \prod_y \frac{1}{\sqrt{2\pi}\rho}\exp\left(-\frac{(\mu_y-\chi)^2}{2\rho^2}\right)$$

where χ and ρ are the hyper-mean and hyper-standard deviation, respectively, of the prior probability distribution for the mean run timing parameters.

The penalty on χ is also normally distributed:

$$(12)\quad L(\chi\,|\,\psi,\xi) = \frac{1}{\sqrt{2\pi}\xi}\exp\left(-\frac{(\chi-\psi)^2}{2\xi^2}\right)$$

where ψ and ξ are the mean and standard deviation of the hyper-prior, respectively, for the hyper-parameter χ. ψ was set to the mean of the estimates of $\{\mu_{1969},\ldots,\mu_{2003}\}$ when no prior is placed on these parameters, and ξ was set to 20. These choices for ψ and ξ were made so that this prior was very uninformative about χ.

The penalty for ρ follows an inverse chi-square distribution:

$$(13)\qquad L(\rho|\nu,s^2)=\frac{\left(\frac{\nu}{2}\right)s^{\nu}\exp\left(-\frac{\nu s^2}{2\rho^2}\right)}{\Gamma\left(\frac{\nu}{2}\right)\rho^{\nu+2}}$$

where ν and s^2 are the mean and variance, respectively, of the hyper-prior on the hyper-parameter ρ (Dorn 2002). The values assumed for the ν and s^2 (7 and 9, respectively) were chosen so that the prior forces the value of ρ away from zero, while allowing the penalty to nevertheless remain informative.

The penalty for the deviation of the process error parameters from zero (i.e., the deviation of the arrival curve from a normal distribution) is assumed to be log-normally distributed:

$$(14)\qquad L(\cdot|\sigma_P)=\prod_y\prod_i\frac{1}{\sqrt{2\pi}\,\sigma_P}\exp\left(-\frac{P_{i,y}^2}{2\sigma_P^2}\right)$$

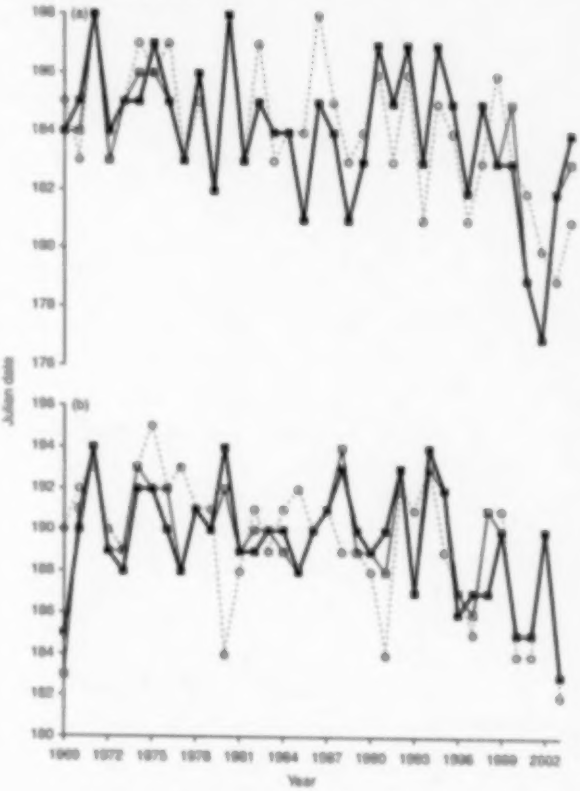
where σ_P is the standard deviation of the process errors.

The objective function also includes a penalty for the deviation of the residence time in the commercial fishing district from its expected value. However, rather than penalizing the mean residence time in the river at the start of the season, $\lambda_{f,y}$, a penalty is instead placed on the deviation of the mean residence time on Julian day 185 (a day chosen to be near the date on which the migration peaks in the commercial fishery) from its expected value. The penalty function for $\lambda_{185,y}$ is therefore

$$(15)\qquad L(\lambda_{185}|\mu_{\lambda_{185}},\sigma_{\lambda_{185}})=\prod_y\frac{1}{\sqrt{2\pi}\,\sigma_{\lambda_{185}}}\exp\left(-\frac{(\lambda_{185,y}-\mu_{\lambda_{185}})^2}{2\sigma_{\lambda_{185}}^2}\right)$$

where $\mu_{\lambda_{185}}$ and $\sigma_{\lambda_{185}}$ are the mean and standard deviation, respectively, of the prior on the in-river residence time on Julian day 185. Because Don Rogers' estimated lag times can be thought of as the sum of district and in-river pooling times, the value of $\mu_{\lambda_{185}}$ was set to the mean lag time estimated for each river by Don Rogers (5.6 and 7.6 days for Egegik and Ugashik rivers, respectively) minus the fixed in-river travel times estimated by ADF&G (2 and 3 days for Egegik and Ugashik rivers, respectively). Don Rogers' method implicitly ignores pooling time before catches occur, and thus the estimates are not wholly comparable. However, we are aware of no studies estimating pooling time in Bristol Bay commercial fishing districts and thus acknowledge the potential bias and proceed with the information available. The value $\sigma_{\lambda_{185}}$ of was set to the standard deviation of the lag times estimated for each river by Don Rogers (1.6 and 1.3 days for Egegik and Ugashik rivers, respectively). Basing the values for $\mu_{\lambda_{185}}$ and $\sigma_{\lambda_{185}}$ on the estimates obtained, Don Rogers' model could be considered to "double use" of some of the data. However, this is not a concern because Don Rogers' model estimates are used to determine a mean (over years) residence time. An invalid use of Don Rogers' estimates would be to use these estimates to obtain year-specific priors where the prior for each year was based on Don Rogers' estimate for the year concerned.

Fig. 5. Median run timing estimates for (*a*) the Egegik District and (*b*) the Ugashik District, 1969–2003, for three levels of process error variance, σ_P = 0 (open circles), 0.3 (open squares), and 0.5 (solid squares).

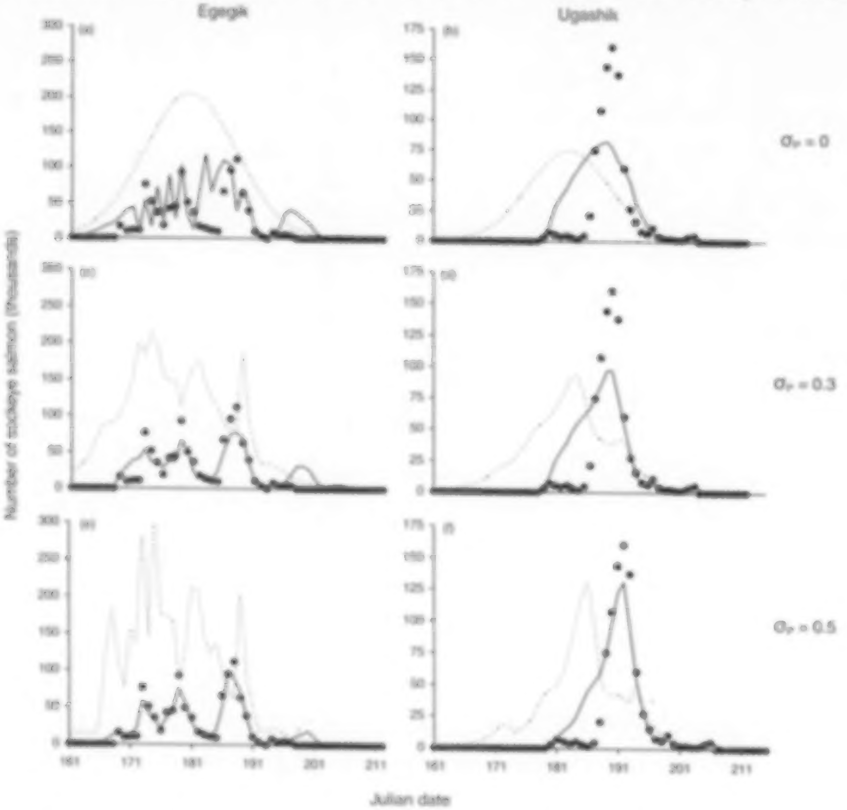


The penalty for catching "unavailable" fish is

$$(16)\qquad P(\cdot|\sigma_v,\boldsymbol{\mu},\boldsymbol{\sigma},\cdot,\boldsymbol{\lambda}_f,\boldsymbol{\lambda}_l)=\prod_y\prod_j\frac{1}{\sqrt{2\pi}\left(\sigma_v h_{j,y}\sum_i D_{i,j,y}+K_v\right)}\times\exp\left(-\frac{\left(C_{j,y}-h_{j,y}\sum_i D_{i,j,y}\right)^2}{2\left(\sigma_v h_{j,y}\sum_i D_{i,j,y}+K_v\right)^2}\right)$$

where $h_{j,y}\sum_i D_{i,j,y}$ is the model estimate of the number of fish harvested on day j of year y. The standard deviation of the "overcatch" penalty is set to $\sigma_v h_{j,y}\Sigma_i D_{i,j,y}+K_v$. The value of σ_v was set to 0.5, as it is not possible to estimate

Fig. 6. Fits to the data for 2001 for three levels for the extent of process error (σ_P): model-predicted arrivals to the commercial fishing district ($A_{i,y}$; broken line), model-predicted tower counts ($\hat{T}_{k,y}$; solid line), and observed tower counts ($T_{k,y}$; solid circles).



this parameter in conjunction with the other parameters of the model. This value of σ_v penalized cases in which the model-estimated catches were less than the actual catches, but not to such an extent that this penalty dominated the objective function. The constant K_V (set to 0.1) is included in eq. 16 so that an inability to fit small catches is not overweighted relative to an inability to fit large catches.

Four model runs were conducted for each river system: three with different levels of process error (σ_P = 0.0, σ_P = 0.3, σ_P = 0.5) and one with σ_P = 0.5 in which the penalties related to the hyper-prior associated with the values for the vector $[\mu_{1969}, \ldots, \mu_{2003}]$ (penalties *ii*, *iii*, and *iv* above) were excluded (Table 1). The values of $\sigma_{T,y}$ were estimated in all cases.

Results

A visual assessment of the median run timing estimates indicates that the addition of process error impacts the results slightly in many years and substantially in several years, particularly for the Ugashik district (Fig. 5). A closer examination of model fits indicates that ignoring process error may lead to an inability to mimic the escapement data. We show the fits to the data for 2001, chosen as a representative year, for the three levels of process error variance (σ_P = 0, 0.3, and 0.5; Fig. 6). Setting σ_P to 0 or 0.3 led to fairly adequate fits to the data for the Egegik district. For this district, increasing σ_P to 0.5 simply decreases the amount of observation error, σ_T. However, setting σ_P to 0 or 0.3 for the Ugashik district results in a (subjectively judged) failure to fit the data, and even at σ_P = 0.5, the model overpredicts the early escapements.

An additional consideration is that more fish are lost to overcatch at low levels of process error. The interannual average harvest rate by decile of the run is shown (Fig. 7; results are shown by decile because harvest rates are high and variable from day to day within each season). The model mimics the catches better, and thus harvest rates are higher as process error is increased from 0 to 0.3 for Egegik. However, for Ugashik, both the addition of process error and increasing it from 0.3 to 0.5 increased harvest rates for most deciles. These results suggest that a greater extent of process error is needed to satisfactorily fit the data for the Ugashik district.

There is a strong relationship between the run reconstruction estimated median and mean arrival dates (Fig. 8), which suggests that the arrival distributions are not strongly or consistently skewed. The uncertainty of the run timing estimates is quantified through the asymptotic standard deviations for the estimates of the mean arrival date $\bar{A}_{i,y}$. These are relatively small compared with the interannual variation in $\bar{A}_{i,y}$ (shown for $\sigma_P = 0.5$ in Fig. 9). The standard deviation in estimated mean run timing among years was 2.1 and 2.7 days for Egegik and Ugashik, respectively, and the widths of the 95% confidence intervals for the estimated mean run timings for each river averaged 0.2 and 0.7 days for Egegik and Ugashik, respectively. Thus, it appears that the data are quite informative regarding mean run timing.

The model fits and the estimates of mean run timing are robust to placing a prior on the values for the vector $[\mu_{1980},\ldots,\mu_{2003}]$. When median run times were estimated both with and without priors ($\sigma_P = 0.5$ in both cases), estimates for each district differed only by 1 day in 1 year. This suggests that the penalties imposed on mean running times are dominated by the data. This is perhaps not surprising because there is a large amount of information for each year and considerable interannual variation in mean run timing among years. The hyper-prior therefore provides very little information relative to the data for each year. The inclusion of the hyper-parameters remains a useful exercise, however, because it aids in identifying the years in which the model fits the data particularly poorly so the estimates are "shrunk" to the mean, and it can provide an expected mean return timing for a new year when additional data are not available. Results indicate that the expected median run timing in the absence of additional data is approximately Julian date 184 (3 July) for Egegik and Julian date 189 (8 July) for Ugashik.

The values of the (derived) mean district residence time parameters on 4 July, λ_{185}, appear to be well-defined, with relatively narrow asymptotic 95% confidence intervals compared with the extent of interannual variation in the parameter estimates (Fig. 10). Although the λ_{185} values for each district display a slight increase over the time series, the slope is quite small relative to interannual variation, particularly in the case of Ugashik. This trend may be indicative of a gradual change in conditions encountered by the migrating fish, as one could conjecture that warmer ocean temperatures result in earlier returning fish, which then hold off the river mouths for a longer period before entering fresh water.

A visual examination of model fits to the data for all years (not shown because of space constraints) indicated that, in general, model fits to the escapement data were generally better later in the time series. This phenomenon may be due to the relatively large catches in the later years (see Fig. 2), where the run (and thus the likelihood surface) is dominated by a single data source, that of the catches.

Reconstruction results were very similar to those produced by Rogers, whereas the results from ADF&G's method suggested generally later run timing, as expected because escapements are not moved back in time to when they would have been in the fishery (Fig. 11). The Rogers' estimates and the run reconstruction results are closer to those of ADF&G in the most recent years, as both Rogers' lag time estimates and run reconstruction mean pooling time estimates are smaller in those years.

Discussion

It seems clear that it is necessary to include process error when modeling run timing for sockeye salmon in Bristol Bay and, hence, that models of the type developed by Schnute and Sibert (1983) are only useful in the case of Bristol Bay with the addition of process error. In the case of the Egegik district, it appears that the underlying distribution is reasonably normally distributed, with process error likely due to factors that are not accounted for in the model such as shifts in tides, currents, or salinity distribution. However, in the case of the Ugashik district, many estimated arrival patterns are dominated by one or two sharp spikes in arrival dwarfing arrivals on all other days, rendering the underlying normal distribution essentially meaningless. Moreover, the model occasionally fails to fit the Ugashik data well, even at $\sigma_P = 0.5$. The two rivers would theoretically be expected to display similar patterns. However, it is also possible that this is not the case. For example, the Ugashik run may be a significant interceptor of fish enroute to other districts (such as Egegik or Kvichak) or may be affected by significant interception elsewhere, as discussed below.

The combination of the model's hierarchical structure and the inclusion of process error led to an extremely large num-

Fig. 7. Interannual average harvest rate by decile of the run for (*a*) Egegik and (*b*) Ugashik for three levels of process error variance, $\sigma_P = 0$ (bold line), 0.3 (thin line), and 0.5 (dotted line).

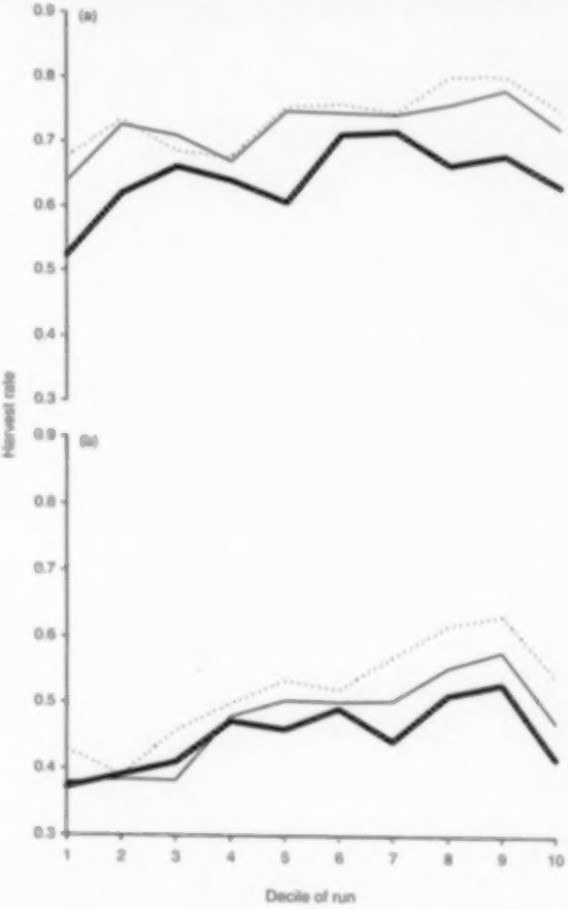


Fig. 8. Comparison of median and mean (μ_y) run timing estimates for (*a*) Egegik and (*c*) Ugashik for $\sigma_p = 0.5$, and plots of the residuals from those relationships against year (*b* and *d* for Egegik and Ugashik, respectively).

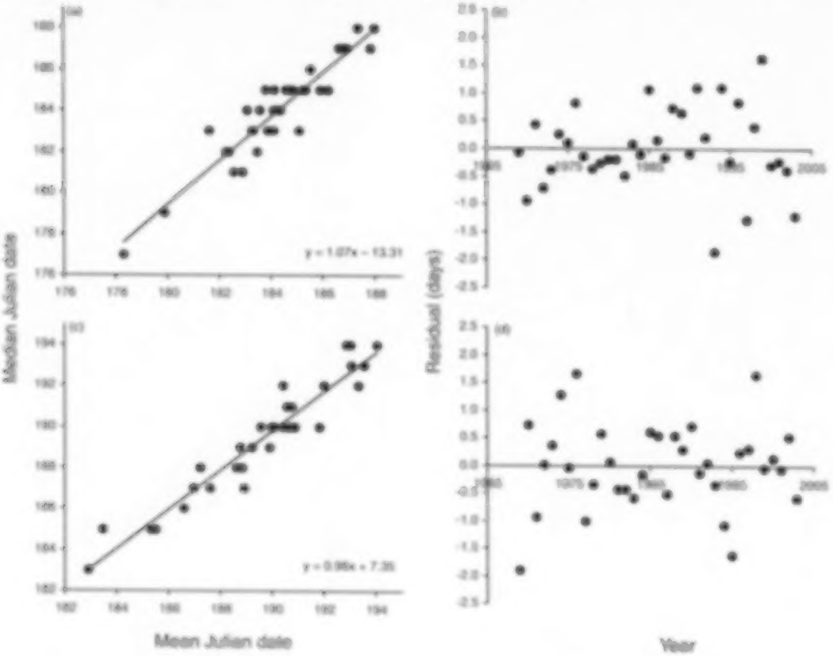
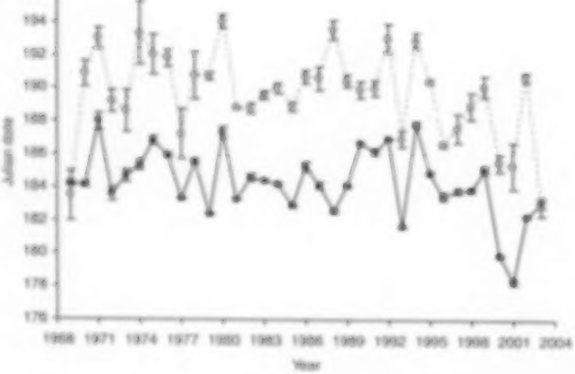


Fig. 9. Mean run timing estimates (μ_y) for Egegik (solid circles) and Ugashik (open circles) and their associated asymptotic 95% confidence intervals. The results in this figure are based on the assumption $\sigma_p = 0.5$.



ber of estimable parameters, 1997 and 2102 for Egegik and Ugashik, respectively. Although this creates no theoretical problem, implementation is a concern. It is unlikely that many more parameters could be estimated with confidence that the actual minimum of the objective function is obtained, and the amount of time required to numerically integrate over the parameter surface to determine, e.g., a Bayesian posterior for the hyper-parameters would be prohibitive. Because our results indicate that there is little to be gained by imposing a hierarchical structure on the parameters that determine mean run timing anyway, it seems reasonable to apply the model to each year separately, ignoring the prior imposed on the mean run timing parameters.

There are also several directions for further model development. For example, ADF&G performs test fishing to estimate in-river abundance several times each day during the fishing season and often also performs test fishing in the commercial fishing districts when they are closed to commercial fishing. Furthermore, management biologists frequently fly the rivers and estimate the number of fish in-river visually. These additional data sources, once captured electronically, could be included when estimating the parameters of the model, although this would require estimation of some catchability–observability parameters.

Several additional research questions also present themselves. For example, early season catches in Ugashik, the run timing of which is later than those of the Egegik, Naknek–Kvichak, and Nushagak districts, may consist of a large number of fish intercepted enroute to another district. A multidistrict model (e.g., Egegik and Ugashik together) could attempt to model interception, and information on the stock composition of district catches is becoming available as genetic stock identification techniques are implemented. Additionally, there is evidence that the Ugashik run is subject to greater levels of intercept by North Peninsula fisheries than are the other districts (i.e., Straty 1975; Geiger 1989; Menard and Miller 1997), although ADF&G has concluded that none of these studies was designed in such a way as to provide definitive evidence. Although our analysis was clearly not designed to test such a hypothesis, there may be value in comparing the arrival pattern of fish to the Ugashik

Fig. 10. Estimated mean district pooling times on Julian date 185 (λ_{185}) for (*a*) Egegik and (*b*) Ugashik and their associated asymptotic 95% confidence intervals. The results in this figure are based on the assumption $\sigma_p = 0.5$.

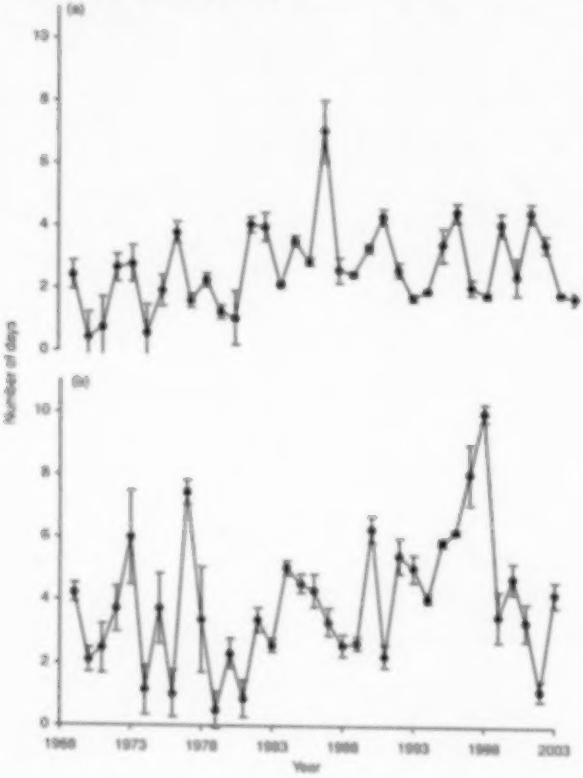
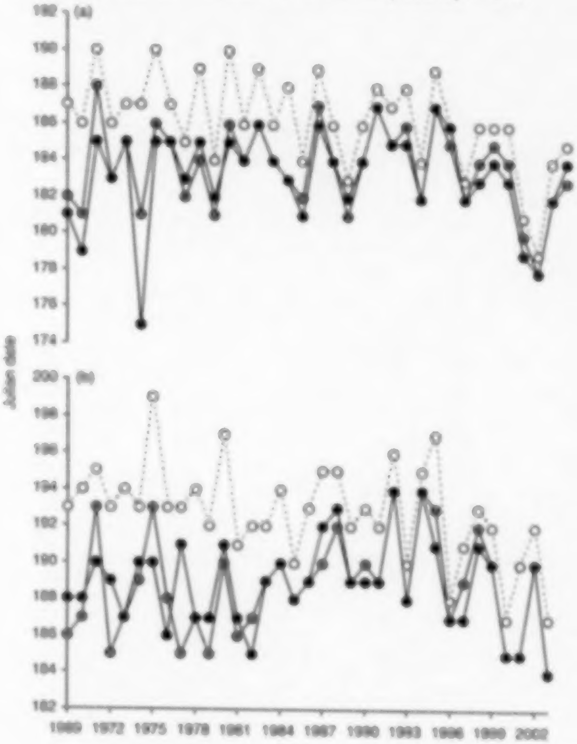


Fig. 11. Median run timing estimates for (*a*) Egegik and (*b*) Ugashik obtained using the Alaska Department of Fish and Game's constant lag time method (open circles), Rogers' visually estimated lag times (shaded circles), and the run reconstruction method of this paper (solid circles). The results for the run reconstruction method are based on the assumption $\sigma_p = 0.5$.



district with the corresponding sockeye salmon catches on the North Peninsula and Egegik.

Additionally, although many studies have evaluated the relationships between Pacific salmon run timing and environmental covariates (i.e., Mundy 1982; Blackbourn 1987; Xie and Hsieh 1989) and several specifically for the Bristol Bay sockeye salmon run (Fujii 1975; Burgner 1980; Hodgson 2000), the harvest rates calculated above will allow the posing of a slightly more complex question: Does the pattern of harvest within the fishing season consistently select for fish returning at some run timing relative to the rest of the run, and if so, has that affected run timing response to environmental variables?

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Appendix A

Table A1. Model notation.

Data	
$C_{i,y}$	Commercial catch on day *i* of year *y*
$T_{k,y}$	Tower count (escapement) on day *k* of year *y*
Parameters	
χ	The hyper-mean of arrival timing
ρ	The hyper-standard deviation of arrival timing
μ_y	Mean arrival timing during year *y*
σ_y	Standard deviation of arrival timing during year *y*
$P_{i,y}$	Process error for day *i* of year *y*
σ_P	Interannual coefficient of variance in process error (prespecified)
σ_v	Coefficient of variance in overcatch, the amount by which the catch on a given day is greater than the model number of available fish on that day (prespecified)
$\lambda_{f,y}$	Mean of the normally distributed residence time in the district for the first day of the season (Julian date 161) of year *y*
$\lambda_{l,y}$	Mean of the normally distributed residence time in the district on the last day of the season (Julian dates 212 and 215 for Egegik and Ugashik, respectively) of year *y*
σ_λ	Standard deviation of the residence time in the district (prespecified)
θ	Mean residence time in the river for all years and all arrival dates

Table A1 (*concluded*).

σ_θ	Standard deviation of the residence time in river (prespecified)
$\sigma_{T,y}$	Coefficient of variance in the tower counts (escapement) for year y
Intermediate variables	
S_y	Run size during year y
$A_{i,y}$	The number of fish arriving into the district on day i of year y
$D_{i,j,y}$	The number of fish that arrived into the district on day i of year y and are still present on day j
$h_{j,y}$	Harvest rate for day j of year y
$m_{x,i,y}$	Proportion of fish leaving the commercial fishing district after x days of residence, having arrived on day i of year y
$R_{j,k,y}$	Number of fish that entered the river on day j and are still present on day k of year y
n_x	Proportion of fish leaving the river after x days of residence
$\hat{T}_{k,y}$	Model estimate of the number of fish passing the counting tower on day k of year y
Miscellaneous constants	
α	= 2.8168; used to convert $h^{o}_{i,y}$ into $h_{i,y}$ (see eq. 3*b*)
β	= 0.11013; used to convert $h^{o}_{i,y}$ into $h_{i,y}$ (see eq. 3*b*)
K_H	= 1×10^{-10}; used to avoid numerical instabilities during implementation of harvest rate transformation function (see eq. 3*b*)
K_v	= 0.1; minimum standard deviation in overcatch, the harvest in excess of available fish (see eq. 16)
K_T	= 0.1; minimum standard deviation in the difference between expected and observed escapements (see eq. 10)
$x_{\min}$, $x_{\max}$	= 1, 15; minimum and maximum possible number of days spent pooling in the commercial fishing district (see eq. 5)
$w_{\min}$, $w_{\max}$	= 1, 5; minimum and maximum possible number of days spent pooling in river (see eq. 8)
Penalty function values	
ψ	Mean of the probability distribution for the penalty on χ, the hyper-mean for the mean date of arrival
ξ	Standard deviation of the prior probability distribution on χ, the hyper-mean for the mean date of arrival
ν	Mean of the probability distribution for the penalty on ρ, the standard deviation for the mean date of arrival
s^2	Variance of the probability distribution for the penalty on ρ, the standard deviation for the mean date of arrival
$\mu_{\lambda_{185}}$	Mean of the probability distribution for the penalty on $\{\lambda_{185,1969},\ldots,\lambda_{185,2003}\}$, the vector of mean fishing district residence times for fish arriving in the district on Julian date 185
$\sigma_{\lambda_{185}}$	Standard deviation of the probability distribution for the penalty on $\{\lambda_{185,1969},\ldots\lambda_{185,2003}\}$, the vector of mean fishing district resident times for fish arriving in the district on Julian date 185

Translating restoration scenarios into habitat conditions: an initial step in evaluating recovery strategies for Chinook salmon (*Oncorhynchus tshawytscha*)

Krista K. Bartz, Kerry M. Lagueux, Mark D. Scheuerell, Tim Beechie, Andrew D. Haas, and Mary H. Ruckelshaus

Abstract: One of the challenges associated with recovering imperiled species, such as Chinook salmon (*Oncorhynchus tshawytscha*), is identifying a set of actions that will ensure species' persistence. Here we evaluate the effects of alternative land use scenarios on habitat conditions potentially important to Chinook salmon. We first summarize the alternative scenarios as target levels for certain land use characteristics. We then use the target levels to estimate changes in current habitat conditions. The scenarios we explore indicate considerable potential to improve both the quality and quantity of salmon habitat through protection and restoration. Results from this analysis constitute the habitat inputs to a population model linking changes in habitat to salmon population status. By transparently documenting the approach we use to translate land use actions into changes in salmon habitat conditions, we provide decision makers with a clear basis for choosing strategies to recover salmon.

Résumé : Un des défis reliés à la récupération d'espèces menacées, comme le saumon chinook (*Oncorhynchus tshawytscha*), est d'identifier un ensemble d'actions qui assurera la persistance de l'espèce. Nous évaluons ici les effets de scénarios de rechange d'utilisation des terres sur les conditions des habitats potentiellement importants pour le saumon chinook. Nous commençons par définir les scénarios de rechange en relation avec des niveaux-cibles dans les conditions d'utilisation des terres. Nous utilisons ensuite les niveaux-cibles pour estimer les changements dans les conditions actuelles d'habitat. Les scénarios étudiés offrent un potentiel considérable pour l'amélioration tant de la qualité que de la quantité des habitats de saumon par le moyen de mesures de protection et de restauration. Les résultats de l'analyse servent de variables d'entrée de l'habitat dans un modèle démographique qui relie les changements de l'habitat au statut démographique du saumon. En décrivant de façon explicite notre méthodologie pour relier les actions prises sur les terres à des conditions d'habitat pour le saumon, nous fournissons aux gestionnaires responsables des décisions une base claire dans leur choix de stratégies pour la récupération des saumons.

[Traduit par la Rédaction]

Introduction

One of the most significant challenges associated with recovering imperiled species is identifying the set of actions needed to ensure species' persistence. Except in rare cases in which the primary factors limiting species recovery are discrete, such as the reduction in harvest of whales or the restoration of host plant populations for butterflies (Schultz 2001; Urbán et al. 2003), the myriad causes of species' decline make it difficult to choose strategically among potential recovery actions. Indeed, the primary cause of imperilment for species listed under the US Endangered Species Act (ESA) is habitat loss and degradation (Wilcove et al. 1998), which typically threaten species' status in a piecemeal, "death by a thousand cuts" fashion (Lawler et al. 2002). A key question for recovering such species is, which of the thousand potential sources of imperilment should be targeted to improve species status?

The widespread and relatively general nature of threats associated with habitat loss and degradation forces biologists designing recovery strategies to answer difficult questions about where and how much habitat protection or restoration is needed for species recovery. Addressing these questions requires two main steps of analysis: (*i*) estimating the

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effects of potential management actions on the quality and quantity of habitat, and (*ii*) evaluating the cumulative effects of changes in habitat quality and quantity on species' status (Fig. 1; Beechie et al. 2003). In this paper, we illustrate an analytical approach for the first of these two steps using Chinook salmon (*Oncorhynchus tshawytscha*) as our focal species. The second step in the analysis, designed to evaluate the effects of recovery strategies on species' status, is described in a companion paper, Scheuerell et al. (2006).

Evaluating recovery strategies for Chinook salmon

Chinook salmon in the Puget Sound region were listed as a threatened species under the ESA in 1999 because of declining population trends, reduction in the number of adults returning to spawn, and loss of life-history diversity (Myers et al. 1998; NMFS 1999). Subsequent to the listing, a NOAA Fisheries-appointed Technical Recovery Team identified 22 demographically independent populations of Chinook salmon still extant within the Puget Sound region (Ruckelshaus et al. 2006). Since then, stakeholders throughout the region have been charged with developing population-specific recovery strategies.

The development of population-scale recovery strategies for salmon is widespread throughout the Pacific Northwest (Ruckelshaus et al. 2002). Related to this development is a need to understand how management actions may degrade or restore salmon habitat. Fortunately, many empirical studies link management actions on land to instream habitat conditions (Table 1); unfortunately, most of these studies demonstrate responses in small catchments to a limited number of actions, producing results that may or may not be transferable to other locations (Swank and Johnson 1994). Therefore, despite the widespread need to estimate the effects of actions on habitat, few studies address the scale, number of treatments, or range of locations necessary for designing and evaluating recovery strategies for salmon populations.

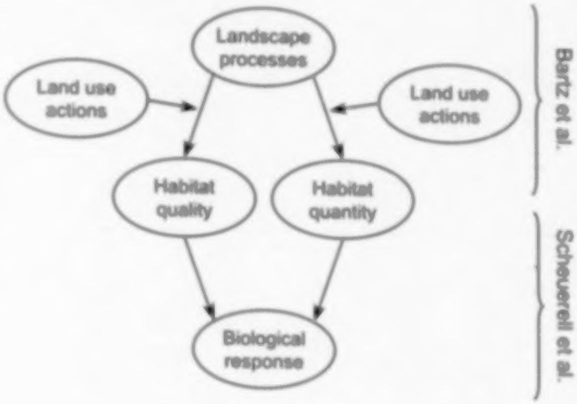
In this paper, we evaluate the effects of alternative suites of management actions on habitat conditions potentially important to Chinook salmon populations. We first summarize three alternative suites of actions, expressed as "target levels" for certain land use characteristics. We then use the target levels for each alternative to estimate changes in current habitat conditions. In particular, we focus on two broad types of habitat conditions: those related to habitat quality (specifically, stream temperature, stream flow, and streambed sediment) and those related to habitat quantity (specifically, potential juvenile and adult capacity).

Materials and methods

Study area

The Snohomish basin is located in the northwestern corner of Washington State (Fig. 2). It has a drainage area of 4780 km^2, extending from the crest of the Cascade Range in the east to Puget Sound in the west and is comprised of three main rivers: the Snohomish, the Skykomish, and the Snoqualmie. Annual precipitation ranges from 94 to 311 cm. Elevation ranges from 0 to 2427 m above sea level. Two of the 22 Chinook salmon populations of Puget Sound inhabit the basin. Other anadromous salmonids in the basin include steelhead (*Oncorhynchus mykiss*), bull trout (*Salvelinus confluentus*), and coastal cutthroat trout (*O. clarkii clarkii*), as well as coho (*O. kisutch*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon (Pacific Groundwater Group 1995). Historically, anadromous access to 40% of the basin was blocked by two natural barriers, Sunset Falls and Snoqualmie Falls. Since 1958, the barrier at Sunset Falls has been circumvented by trapping and hauling spawning salmonids upstream.

Fig. 1. Diagram of the analytical step taken in this paper (estimating the effects of land use actions on the quality and quantity of habitat) and a subsequent step in the companion paper by Scheuerell et al. (2006; evaluating the cumulative effects of changes in habitat quality and quantity on salmon status). The diagram is adapted from Beechie et al. (2003).



The basin is divisible into 62 subbasins defined primarily by topography and drainage patterns (Fig. 2; Gersib et al. 1999). Land cover varies widely between subbasins, with forest cover ranging from 7% to 83% and impervious cover ranging from 0% to 49%, according to a classification by Purser et al. (2003). Given recent rates of land cover change (Simmonds et al. 2004) and a predicted 50% increase in the local human population by 2020 (Puget Sound Regional Council et al. 1992), forest cover will likely decrease in the future as impervious cover increases. Such changes are expected to further disrupt the physical, chemical, and biological processes that create and sustain salmon habitat over time (Fig. 1; Meehan 1991). The alternative suites of management actions (i.e., alternative scenarios) explored in this paper address these predicted impacts on salmon habitat.

Approach

We generated changes in salmon habitat conditions under the alternative scenarios in four steps. Step 1 involved developing the alternative scenarios. Steps 2 and 3 entailed estimating changes in habitat quality and quantity attributes, based on the target levels for each scenario. In Step 4, we computed confidence intervals for the point estimates from the previous two steps. The point estimates then served as inputs to Shiraz, a life cycle model described by Scheuerell et al. (2006). Because Scheuerell et al. chose the subbasin as the level of spatial resolution for Shiraz, we also used the subbasin as our unit of analysis.

Table 1. Results from previous studies linking land use variables to salmon habitat conditions in the Northwest.

Land use variable	Salmon habitat condition					
	Stream temperature		Peak stream flow		Streambed fines	
	Response	Source(s)[a]	Response	Source(s)[a]	Response	Source(s)[a]
Road density	0	*	0	1–7	0	9, 10
	+	*	+	1, 5	+	9, 11–13
	–	*	–	8	–	*
Impervious cover	0	14	0	*	0	*
	+	*	+	15–17	+	18
	–	*	–	*	–	19
Forest cover[b]	0	*	0	1–5, 7, 8, 23	0	*
	+	*	+	*	+	*
	–	2, 14, 20–26	–	1–8, 23, 27–30	–	31, 32

Note: Results are expressed as responses of habitat conditions to increases in land use variables. Responses may be positive (+), negative (–), or nonexistent (0) and are compiled mainly from reviews by Hollis 1975, Beschta et al. 1987, Wright et al. 1990, Moore and Wondzell 2005, and Moore et al. 2005.

[a] Sources: *, no known studies report this response; 1, Harr et al. 1975; 2, Harris 1977; 3, Harr 1983; 4, Ziemer 1981; 5, Wright et al. 1990; 6, Jones and Grant 1996; 7, Thomas and Megahan 1998; 8, Rothacher 1973; 9, Duncan and Ward 1985; 10, Bilby et al. 1989; 11, Reid 1981; 12, Reid and Dunne 1984; 13, Cederholm and Salo 1979; 14, Booth et al. 2001; 15, James 1965; 16, Booth and Jackson 1997; 17, Law 1994; 18, Olthof 1994; 19, Finkenbine et al. 2000; 20, Levno and Rothacher 1969; 21, Brown and Krygier 1970; 22, Brown et al. 1971; 23, Harr et al. 1979; 24, Feller 1981; 25, Harr and Fredriksen 1988; 26, Johnson and Jones 2000; 27, Anderson and Hobba 1959; 28, Hetherington 1982; 29, Harr et al. 1982; 30, Hudson 2001; 31, Platts et al. 1989; 32, Eaglin and Hubert 1993.

[b] Most studies describe responses to decreases in forest cover; we state the inverse of those responses here.

Step 1: generating the alternative scenarios

The Snohomish Basin Salmonid Recovery Technical Committee (SBSRTC), a local scientific advisory group, developed two alternative future scenarios to explore possible strategies for salmon recovery: the "current path" and the "test case" (SBSRTC 2004). The current path assumes that present rates of habitat protection, restoration, and degradation continue for the next 25 years. The test case assumes the implementation of protection and restoration actions that are hypothesized to achieve recovered population status for Chinook salmon, as well as benefits for other salmonid species. Both scenarios depict the future landscape in the basin in terms of target levels for eight land use characteristics (i.e., anthropogenic barriers, edge habitat, off-channel habitat, habitat structures, road density, impervious cover, riparian forest cover, and total forest cover; Table 2). For simplicity, the SBSRTC assigned the target levels to groups of subbasins, rather than individual subbasins (Fig. 2). These groupings were based on subbasin location and landform, as well as the level of fish use and the condition of landscape processes (SBSRTC 2004).

In addition to the two future scenarios, we devised a historical scenario to provide a baseline of land use characteristics against which the current path and test case could be measured (Table 2). We assumed that no anthropogenic barriers existed historically and that no edge or off-channel habitats were filled, armored, or otherwise modified. We also assumed that historical road density and impervious cover resulting from development were 0 km·km^{-2} and 0%, respectively. Historical total forest cover was estimated as 100% minus those areas currently classified as open water, alpine rock, or unknown (Purser et al. 2003). Historical riparian forest cover was estimated from current riparian forest cover, assuming the same historical-to-current ratio as for total forest cover.

Step 2: generating changes in habitat quality under the alternative scenarios

We translated the alternative scenarios into changes in four habitat quality attributes related to salmon survival: (1) stream temperature during the prespawning period (mid-July to mid-October; PNRBC 1981), (2) stream temperature during the egg incubation period (mid-September to mid-February; PNRBC 1981), (3) peak stream flow during the egg incubation period, and (4) fine sediment in the stream bed. Our methods for generating these changes involved two tasks. First, we developed statistical models to estimate the habitat quality attributes under current conditions, then we used the models as templates to produce alternative values for the attributes under each scenario.

Current template

To develop statistical models for estimating the four habitat quality attributes under current conditions, we compiled empirical data for each attribute. Data were drawn from temperature gages, flow gages, and sediment measurements located mainly in the Snohomish basin (Table 3; see also Tables S1–S4[3]). Data from three adjacent basins also were included to bolster the sample sizes, which were small because we limited the data to gage records and sediment measurements collected from the 1990 water year onward in order to approximate the time period in which the independent variables were quantified. The independent variables consisted of four land use characteristics from Table 2 (road density, impervious cover, riparian forest cover, and total forest cover) and five geomorphic characteristics (elevation,

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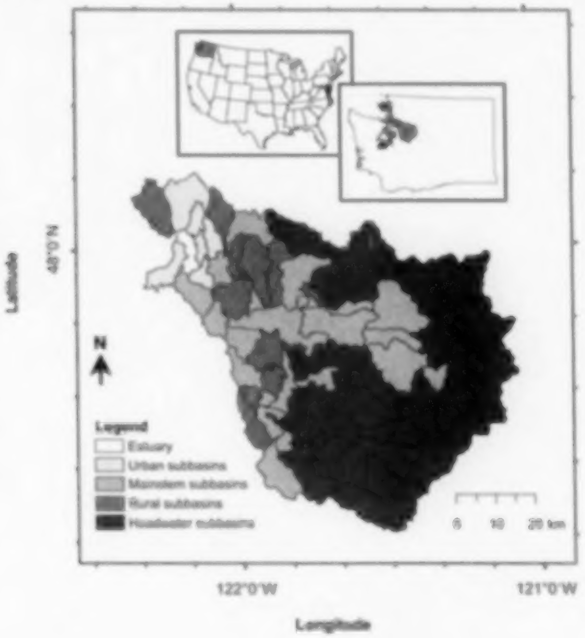
[3] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5036. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Fig. 2. Map of the Snohomish basin in Washington State, USA. The Snohomish Basin Salmonid Recovery Technical Committee organized the 62 subbasins into 11 groups based, in part, on subbasin location (e.g., estuary, urban, mainstem, rural, or headwater areas).



drainage area, channel gradient, mean annual precipitation, and the percentage of alluvium in the surficial geology). Data for land use and geomorphic characteristics were derived through geographic information systems (GIS; Table 3; see also Table S5[3]).

For three of the habitat quality attributes (prespawning temperature, incubation temperature, and fine sediment), we built a candidate set of 82 models that contained all possible linear models with three or fewer independent variables, excluding those models with no land use characteristics and those with more than one strongly correlated land use characteristic (impervious cover, total forest cover, riparian forest cover; see Table S6[3]). We then examined the regression coefficients of all land use characteristics in the candidate models. If the signs of the coefficients countered expectations based on empirical studies relating land use and habitat quality (Table 1), then the models were omitted from the candidate set. For each of the remaining models, we computed the second-order variant of Akaike's information criterion (corrected AIC or AIC_c), as well as the AIC_c difference and weight (Akaike 1973; Burnham and Anderson 1998). The AIC_c difference (Δ_i) was computed by subtracting the lowest AIC_c in the candidate set from the AIC_c of the model i. The AIC_c weight (w_i) was computed as

$$(1)\qquad w_i = \frac{\exp\left(-\tfrac{1}{2}\Delta_i\right)}{\sum_{i=1}^{I}\exp\left(-\tfrac{1}{2}\Delta_i\right)}$$

where I was the total number of models in the candidate set. Given Δ_i and w_i, we used two general guidelines to help select the best model. First, the smaller the Δ_i, the larger the w_i, and the higher the probability that i actually is the best model given the data and the set of models considered (Burnham and Anderson 1998). Second, although there is no exact Δ threshold above which a model should not be considered, evidence against a model begins to mount above a Δ value of 2 (Burnham and Anderson 1998). Once a model was selected, residuals were checked to assure that the assumptions of normality and homogeneity of variance were met.

For the fourth habitat quality attribute (peak flow), the candidate set of models included 24 variants of a published equation used to estimate flows at ungaged sites in the Puget Sound region (Sumioka et al. 1998). According to this equation,

$$(2)\qquad Q = aA^bP^c$$

where Q, A, and P denote flow, drainage area, and mean annual precipitation, respectively, and a, b, and c are coefficients. Variants of this equation were created by adding or multiplying individual land use characteristics (see Table S7[3]). As with the other candidate sets, the regression coefficients of the land use characteristics were examined, and models with unexpected coefficients based on the empirical literature were omitted. AIC_c differences and weights were then used to select the model that best fit the data.

Alternative scenarios

To generate habitat quality estimates under the alternative scenarios, we entered the target levels for the land use characteristics from Table 2 into the selected models. We first needed to express these target levels at the scale of individual subbasins, rather than groups of subbasins, in order to match the scale of the sample units in the models. Therefore, we calculated the percent change in a given land use characteristic from current to target conditions at the subbasin group scale, and then we multiplied this percentage by the current land use characteristic at the subbasin scale.

Step 3: generating changes in habitat quantity under the alternative scenarios

We translated the scenarios into changes in two habitat quantity attributes: potential juvenile capacity and potential adult capacity. These attributes represent the maximum possible number of juveniles or adults that a certain area could support, given estimates of habitat quantity and fish density associated with that area. Our methods for generating changes in these attributes followed the same general outline described in step 2: we estimated the attributes under current conditions, and then used these values as templates to produce alternative values under each scenario.

Potential juvenile capacity

Current template

We modified a two-step approach from Beechie et al. (1994) to estimate potential juvenile capacity under current conditions. First, we quantified potential rearing areas by habitat type, and then we multiplied the areas by habitat-type-specific juvenile densities. Habitat types, at the broadest

Table 2. Target levels for land use characteristics under the current path, test case, and historical scenarios.

		Land use characteristics						
Alternative restoration scenario	Subbasin group	Anthropogenic barrier target (% of blocked area restored to accessibility)	Edge habitat target (% of total bank area in a natural state)	Off-channel habitat target (% of historical off-channel/estuarine area reconnected)	Road density target (km of road per km^2 of upland area)	Impervious cover target (% of total impervious area)	Total forest cover target (% of evergreen and deciduous forest classes)[a]	Riparian forest cover target (% of evergreen and deciduous forest classes)[b]
Current path	Estuary	*	41	25	*	9.0	*	11.0
	Mainstems – 1	10	67	10	*	6.8	40.9	56.0
	Mainstems – 2	10	76	5	*	6.7	54.6	74.0
	Rural streams – 1	10	*	0	*	1.9	35.4	62.0
	Rural streams – 2	10	*	0	*	9.0	20.4	60.0
	Urban streams	10	*	0	*	49.3	5.0	20.0
	Headwaters – 1	10	*	0	0.5	0.0	80.0	80.0
	Headwaters – 2	10	*	0	2.1	0.3	70.7	79.0
	Headwaters – 3	10	*	0	0.9	0.0	80.0	84.0
	Headwaters – 4	10	*	0	0.7	0.0	80.0	*
	Headwaters – 5	10	*	0	1.9	2.1	80.0	*
Test case	Estuary	*	90	70	*	6.0	*	50.0
	Mainstems – 1	80	90	70	*	6.0	65.0	80.0
	Mainstems – 2	80	82	50	*	6.0	65.0	75.0
	Rural streams – 1	80	*	50	*	6.0	65.0	70.0
	Rural streams – 2	80	*	50	*	6.0	65.0	60.0
	Urban streams	80	*	0	*	25.0	50.0	60.0
	Headwaters – 1	80	*	0	0.5	0.0	80.0	80.0
	Headwaters – 2	80	*	0	1.2	0.3	75.0	80.0
	Headwaters – 3	80	*	0	0.9	0.0	80.0	84.0
	Headwaters – 4	60	*	0	0.7	0.0	80.0	*
	Headwaters – 5	60	*	0	1.2	1.0	80.0	*
Historical	Estuary	*	100	100	*	0.0	*	69.8
	Mainstems – 1	100	100	100	*	0.0	97.8	82.8
	Mainstems – 2	100	100	100	*	0.0	96.1	88.9
	Rural streams – 1	100	*	100	*	0.0	98.5	99.0
	Rural streams – 2	100	*	100	*	0.0	98.3	93.1
	Urban streams	100	*	0	*	0.0	95.8	89.3
	Headwaters – 1	100	*	0	0.0	0.0	81.0	69.1
	Headwaters – 2	100	*	0	0.0	0.0	95.3	92.2
	Headwaters – 3	100	*	0	0.0	0.0	95.0	86.6
	Headwaters – 4	100	*	0	0.0	0.0	86.5	*
	Headwaters – 5	100	*	0	0.0	0.0	93.4	*

Note: An asterisk (*) indicates that no target level is set, either because it is not applicable to the scenario or because data are not available.

[a] Total forest cover describes the percentage of evergreen and deciduous forest cover for a given subbasin group.

[b] Riparian forest cover describes the percentage of evergreen and deciduous forest cover for the riparian area of a given subbasin group.

Table 3. Variables used to develop models for estimating the four habitat quality attributes.

Variable type	Variable name	Units	Subbasins with data	Source(s)^a
Dependent variables (habitat quality attributes)	Prespawning temperature	Mean of daily maxima (°C)	14	1, 2, 3
	Incubation temperature	Mean of monthly means (°C)	18	2, 3, 4
	Peak flow	Largest daily mean ($m^3 \cdot s^{-1}$)	20	2, 3
	Fine sediment	Mean fraction < ~6.3 mm in diameter (%)	27	5, 6, 7, 8
Independent variables (land use characteristics)	Road density	$km \cdot km^{-2}$	62	9
	Impervious cover	%	62	10
	Total forest cover	%	62	10
	Riparian forest cover	%	62	10
Independent variables (geomorphic characteristics)	Elevation	Mean (m)	62	11
	Drainage area	km^2	62	12
	Channel gradient	Mean (%)	62	11
	Annual precipitation	Mean (cm)	62	13
	Alluvium	%	62	14

Note: Sources of the data are reported for each variable (see also Tables S1–S5 in the NRC data depository[3]). WDOE, Washington Department of Ecology; USGS, United States Geological Survey; SWM, Surface Water Management; WDNR, Washington Department of Natural Resources.

[a] Sources: 1, WDOE 2005; 2, USGS 2005; 3, Snohomish County SWM 2005; 4, K. Bartz, unpublished data; 5, Booth et al. 1991; 6, DeVries et al. 2001; 7, Parametrix, Inc., Perkins Geosciences, Earth Systems, and Harper Houf Righellis, Inc. 2001; 8, Snohomish County SWM 2002; 9, WDNR 2005; 10, Purser et al. 2003; 11, Washington State Geospatial Data Archive 2001; 12, R. Simmonds, Snohomish County Information Services, 3000 Rockefeller Ave., M/S-709, Everett, WA 98201, unpublished data; 13, Daly and Taylor 1998; 14, M. Purser, Snohomish County SWM, 3000 Rockefeller Ave., M/S-607, Everett, WA 98201, unpublished data.

level, were defined as being either freshwater or estuarine. Freshwater habitat was further divided into channel, off-channel, and lake types. Estuarine habitat was divided into forest, scrub shrub, and emergent marsh types. These divisions, and others described below, were made to the finest resolution that was supported by existing density data for juvenile Chinook salmon (Table 4). Therefore, juvenile capacity (J) in a given subbasin was estimated as

$$(3) \qquad J = \sum_{h=1}^{n} (R_h \cdot D_h)$$

where R and D indicate rearing area and juvenile density, respectively, in habitat type h (Beechie et al. 2003).

To quantify channel rearing area under current conditions, we limited our analysis to accessible reaches with gradients <4%, the threshold below which channels exhibit the morphology preferred by salmon (Lunetta et al. 1997; Montgomery et al. 1999). Reach accessibility was determined using GIS data layers of natural and anthropogenic barriers (Washington Department of Fish and Wildlife 2003; Northwest Indian Fisheries Commission 2003; R. Simmonds, Snohomish County Information Services, 3000 Rockefeller Avenue, M/S-709, Everett, WA 98201, USA, unpublished data). Reach gradient was determined using a digital elevation model of the basin (Washington State Geospatial Data Archive 2001). We estimated bankfull and wetted widths for these accessible, low-gradient reaches, as described by Davies et al. (2006). We then partitioned the reaches into three classes based on bankfull width (bfw) (large mainstems (>50 m bfw), small mainstems (10–50 m bfw), and tributaries (<10 m bfw)) and calculated the area of reaches in each class by multiplying reach lengths by wetted widths. Finally, we divided the reach areas in each class into additional habitat subtypes with the potential to support different densities of juveniles (i.e., pools, riffles, glides, backwaters; Table 4; Bisson et al. 1988). These divisions were based on empirical data regarding the relative percentages of the habitat subtypes in the Snohomish and other nearby basins (see Table S8[3]).

To quantify off-channel rearing area under current conditions, we used GIS to identify off-channel features and the knowledge of local biologists to distinguish which features were accessible (M. Boles and K. Anderson, King County Water and Land Resources Division, 201 S. Jackson Street, Suite 600, Seattle, WA 98104, USA, unpublished data; A. Haas and B. Aldrich, Snohomish County Surface Water Management Division, 3000 Rockefeller Avenue, M/S-607, Everett, WA 98201, USA, unpublished data). Off-channel features included all water bodies within the 100-year floodplain and all side channels connecting those water bodies to the main channel. Side channel lengths were multiplied by a width of 5 m to calculate the area of potential juvenile habitat (A. Haas, unpublished data).

We quantified lake rearing area under current conditions by focusing on lakes connected to accessible channel reaches. Those lakes were divided into three size classes: <500 m^2, 500 – 50 000 m^2, >50 000 m^2. Piaskowski and Tabor (2001) reported that Chinook occupied the shallow areas near lake edges (i.e., 1.6–3.7 m from the edge, depending on the lakeshore gradient). Because we did not have bathymetric data for the lakes, we multiplied the mean of these two distances by the perimeter of each lake to estimate lake rearing area.

To quantify estuarine rearing area under current conditions, we partitioned the estuary into forested riverine tidal, estuarine scrub shrub, and estuarine emergent marsh habitat types, as delineated by Haas and Collins (2001). For each habitat type, we used GIS to estimate the areas of main, distributary, and blind tidal channels that were usable by juvenile salmon. In blind tidal channels, the usable area was defined as a percentage of the total area by habitat type (3.0%, 5.6%, and 10.5% for forest, scrub shrub, and emergent marsh habitat types, respectively; Haas and Collins 2001). In main and distributary channels, the usable area was defined

Table 4. Summary of juvenile densities used to estimate the potential capacity of juvenile Chinook salmon (*Oncorhynchus tshawytscha*).

Habitat type	Habitat subtype	Mean density	SD	*N*	Source(s)[a]
Freshwater, large mainstems	Pool	0.072	0.147	13	1–4
Freshwater, large mainstems	Riffle	0.011	0.026	8	1–4
Freshwater, large mainstems	Glide	0.146	0.207	11	1–4
Freshwater, large mainstems	Bar (edge)	0.206	0.203	5	4–6
Freshwater, large mainstems	Backwater	0.520	0.609	8	1, 4–6
Freshwater, large mainstems	Bank, natural	0.875	0.131	3	5
Freshwater, large mainstems	Bank, modified	0.360	0.287	3	5
Freshwater, small mainstems	Pool	0.214	0.242	34	1, 2, 7–9
Freshwater, small mainstems	Riffle	0.040	0.041	20	1, 2, 7, 8
Freshwater, small mainstems	Glide	0.230	0.130	11	1, 2, 7
Freshwater, small mainstems	Backwater	0.818	0.734	37	1, 2, 10
Freshwater, tributaries	Pool	0.505	0.394	19	8, 11
Freshwater, tributaries	Riffle	0.138	0.154	10	11
Freshwater, tributaries	Glide	0.071	0.039	2	12
Freshwater, lakes	$<500\ m^2$	0.009		1	6
Freshwater, lakes	$500 - 50\,000\ m^2$	0.071	0.084	6	12
Freshwater, lakes	$>50\,000\ m^2$	0.088	0.084	22	13
Freshwater, off-channel	Pond	0.032	0.025	5	5, 6
Freshwater, off-channel	Connecting side channel	0.045	0.034	3	6, 12
Estuary	Forested riverine tidal	0.140	0.151	8	5, 14, 15
Estuary	Estuarine scrub-shrub	0.420	0.533	6	5, 16, 17
Estuary	Estuarine emergent marsh	0.141	0.249	123	5, 15, 16, 18–23

Note: Densities are expressed as mean numbers of Chinook·m^{-2}. They are reported by habitat type, along with standard deviations (SD), sample sizes (*N*), and sources.

[a] Sources: 1, Jonasson et al. 1997; 2, Keefe et al. 1995; 3, Don Chapman Consultants 1989; 4, G. Pess, Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112, unpublished data; 5, Hayman et al. 1996; 6, Murphy et al. 1989; 7, Cramer 2001; 8, Scarnecchia and Roper 2000; 9, Johnson et al. 1992; 10, Lister and Genoe 1970; 11, Sekulich 1980; 12, Swales and Levings 1989; 13, Tabor and Piaskowski 2002; 14, Levings et al. 1995; 15, Levy et al. 1979; 16, Korman et al. 1997; 17, Thom et al. 1990; 18, Beamer and LaRock 1998; 19, Levings et al. 1991; 20, Thom et al. 1989; 21, Congleton et al. 1982; 22, Congleton and Smith 1976; 23, Dunford 1975.

as that within 10 m of the bank, based on a National Wetland Inventory map (US Fish and Wildlife Service 2002). Juvenile use is thought to be limited largely to the slow-water margins of main and distributary channels (Hayman et al. 1996), and empirical measurements indicate that 10 m is a reasonable estimate for margins in the Snohomish ($\bar{x}$ = 10.4 m, *n* = 113 margin measurements; M. Rowse, Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Boulevard East, Seattle, WA 98112, USA, unpublished data).

Alternative scenarios

Changes in juvenile capacity from the current template to the alternative scenarios were driven by altering the rearing areas via the target levels in Table 2. For example, the anthropogenic barrier and edge habitat target levels altered the amount of channel area potentially available for rearing under the alternative scenarios (Table 5). Similarly, the off-channel habitat targets altered the amount of off-channel and estuarine areas (Table 5). Two additional changes were made to distinguish historical capacity from that under the current path or test case scenarios. First, the percentages of the various channel habitat subtypes (i.e., pools, riffles, glides, etc.) were modified to reflect percentages at nearby reference sites (see Table S8[3]). Second, off-channel and estuarine rearing areas were estimated from a GIS-based reconstruction of historical habitat in the basin (Collins and Sheikh 2003). No changes were made to the juvenile densities in Table 4 because of a lack of historical density data.

Potential adult capacity

Our approach for estimating the potential of freshwater habitats to support Chinook salmon spawning was based in part on a method for quantifying habitat conditions from remote sensing data (Lunetta et al. 1997) and in part on a method for quantifying potential spawner population size from stream characteristics (Beechie et al. 2006). The approach is described in more detail in the Snohomish basin recovery plan (SBSRTC 2004).

Current template

To estimate potential adult capacity under current conditions, we first determined the width, gradient, and accessibility of each stream reach in the basin as described above for potential juvenile capacity. The amount of accessible habitat was then summed by subbasin in three stream width–gradient classes: (1) bfw >25 m, gradient ≤4%, (2) bfw 5–25 m, gradient <1%, and (3) bfw 5–25 m, gradient 1%–4%. For reaches with >25 m bfw, the amount of habitat was summed by area; for reaches with 5–25 m bfw, the amount of habitat was summed by length. Finally, the amounts of habitat in each width–gradient class were used, along with several density variables, to calculate capacity for each class (Table 6). The density variables included the number of adults per redd (1.9; Holsinger and Pess 2003), the area of each redd (14.1 m^2; Holsinger and Pess 2003), the number of redds/km (31.2; D. Montgomery, University of Washington, Department of Earth and Space Sciences, Box 351310, Seattle, WA

Table 5. Equations used to estimate juvenile rearing area in certain habitat types under the current path and test case scenarios.

Habitat type	Potential juvenile rearing area equation
Freshwater, tributaries	$CA_f = CA_c + [CA_a(\text{anthropogenic barrier target}_f/100)]$
Freshwater, large mainstems	$BA_{n,f} = BA_{t,c}(\text{edge habitat target}_f/100)$
Freshwater, large mainstems	$BA_{m,f} = BA_{t,c} - BA_{n,f}$
Freshwater, off-channel	$OA_f = OA_h(\text{off-channel habitat target}_f/100)$
Estuary	$EA_f = [0.8EA_h(\text{off-channel habitat target}_f/100)] + (0.2EA_h)$

Note: CA, channel area; BA, bank area; OA, off-channel area; EA, estuarine area. Subscripts: f, future scenario, either current path or test case; c, current; h, historical; a, above culvert; n, natural; m, modified; t, total (i.e., natural + modified). Target levels are given in Table 2. The estuarine area equation assumes that 80% of the historical area is currently inaccessible (Haas and Collins 2001).

Table 6. Equations used to estimate potential adult capacity under current conditions for three stream width–gradient classes.

Bankfull width, gradient	Potential adult capacity equation
>25 m, ≤4%	$\text{Capacity} = [(\text{stream area}) \times (\%\ \text{spawnable area}/100) \times (\text{adults}\cdot\text{redd}^{-1})] \times (\text{m}^2\cdot\text{redd}^{-1})^{-1}$
5–25 m, <1%	$\text{Capacity} = (\text{stream length}) \times (\text{adults}\cdot\text{redd}^{-1}) \times (\text{redds}\cdot\text{km}^{-1})$
5–25 m, 1%–4%	$\text{Capacity} = (\text{stream length}) \times (\%\ \text{forced pool–riffle}/100) \times (\text{adults}\cdot\text{redd}^{-1}) \times (\text{redds}\cdot\text{km}^{-1})$

Note: Units for stream area and stream length are m^2 and km, respectively.

98195, USA, unpublished data), the percentage of spawnable habitat (6.2%; Holsinger and Pess 2003), and the percentage of forced pool–riffle habitat. This final variable depended on the seral stage of the riparian vegetation adjacent to the reach (Lunetta et al. 1997). If the stage was late seral, then 100% of the stream length was considered forced pool–riffle habitat. If the stage was mid-seral, early seral, or nonforest, the percentage decreased to 78%, 74%, or 35%, respectively.

Alternative scenarios

To generate adult capacity estimates for the historical scenario, we made several adjustments to the current template. Anthropogenic migration barriers were omitted from the assessment of reach accessibility, and two adult density variables were altered to reflect presumed historical geomorphic conditions. Specifically, the percentage of spawnable habitat increased from 6.2% to 9.7% for reaches with bankfull widths >25 m and gradients ≤4% (Table 6; Holsinger and Pess 2003), and the percentage of forced pool–riffle habitat changed to 92.2% for reaches with bankfull widths of 5–25 m and gradients of 1%–4% (Table 6; Lunetta et al. 1997). To generate adult capacity estimates for the current path and test case scenarios, we used the density values from the current template. Thus, the current path, test case, and current template estimates were indistinguishable.

Step 4: generating confidence intervals for habitat quality and quantity

We used a Monte Carlo simulation approach to account for uncertainty in the habitat quality and quantity point estimates. Each habitat quality attribute was calculated 1000 times per subbasin and scenario by drawing randomly from the distributions of the parameters in the selected model. Similarly, each habitat quantity attribute was computed 1000 times per subbasin and scenario by randomly sampling the density data and then multiplying the resulting sample by the appropriate habitat area or length. We determined the 95% confidence intervals for the means of these 1000 simulations. For some attributes, the simulations were log-transformed to meet normality assumptions, causing the reverse-transformed confidence intervals to be asymmetrical.

Results

We generated habitat quality and quantity estimates for each subbasin to match the spatial resolution used by Scheuerell et al. (2006) in Shiraz. For the sake of simplicity, results are reported primarily at the basin scale here. However, subbasin-scale estimates and confidence intervals are available (Tables S9–S12[3]).

Changes in habitat quality under the alternative scenarios

We selected four statistical models to estimate habitat quality under the alternative scenarios. Three of these models were ranked first in their respective candidate sets, according to AIC_c differences and weights (Δ_i and w_i; Table 7; see also Tables S13–S16[3]). Specifically, the top-ranked prespawning temperature model ($\Delta_i = 0.00$, $w_i = 0.28$, adjusted $R^2 = 0.84$; Tables 7 and 8) was selected over other models with $\Delta_i \leq 2$ because its w_i, although low, was almost 50% greater than that of the next best model. The top-ranked incubation temperature model ($\Delta_i = 0.00$, $w_i = 0.41$, adjusted $R^2 = 0.81$) was selected because it was the only model in the candidate set with $\Delta_i \leq 2$, and because its w_i indicated that it was more than five times as likely as the next best model to be the actual best fit. The top-ranked flow model ($\Delta_i = 0.00$, $w_i = 0.87$, adjusted $R^2 = 0.99$) was selected for the same reasons as the incubation temperature model. However, the second-ranked fine sediment model ($\Delta_i = 0.05$, $w_i = 0.18$, adjusted $R^2 = 0.62$) was selected over the top-ranked model because the w_i values of the two models were nearly identical, and

Table 7. The top five models for each habitat quality attribute, ranked by increasing differences (Δ_i) and decreasing weights (w_i) of the corrected form of Akaike's information criterion (AIC_c).

Habitat quality attribute	Model	AIC_c	Δ_i	w_i
Prespawning temperature	$y = a + b\mathrm{RFC} + c\mathrm{PRECIP} + d\mathrm{ALLUV}$	54.57	0.00	0.28
	$y = a + b\mathrm{RFC} + c\mathrm{PRECIP}$	55.29	0.72	0.20
	$y = a + b\mathrm{RFC} + c\mathrm{PRECIP} + d\mathrm{DA}$	55.42	0.85	0.18
	$y = a + b\mathrm{RFC} + c\mathrm{PRECIP} + d\mathrm{GRAD}$	55.48	0.90	0.18
	$y = a + b\mathrm{TFC} + c\mathrm{PRECIP} + d\mathrm{GRAD}$	56.68	2.10	0.10
Incubation temperature	$y = a + b\mathrm{RD} + c\mathrm{ELEV}$	33.15	0.00	0.41
	$y = a + b\mathrm{RD} + c\mathrm{ELEV} + d\mathrm{RFC}$	36.35	3.20	0.08
	$y = a + b\mathrm{RD} + c\mathrm{ELEV} + d\mathrm{DA}$	36.53	3.38	0.08
	$y = a + b\mathrm{RD} + c\mathrm{ELEV} + d\mathrm{TFC}$	36.53	3.38	0.08
	$y = a + b\mathrm{RD} + c\mathrm{ELEV} + d\mathrm{GRAD}$	36.60	3.45	0.07
Peak flow	$y = a\mathrm{DA}^b\,\mathrm{PRECIP}^c\,\mathrm{IC}^d$	214.38	0.00	0.87
	$y = a\mathrm{DA}^b\,\mathrm{PRECIP}^c\,d\mathrm{IC}^e$	218.56	4.18	0.11
	$y = a\mathrm{DA}^b\,\mathrm{PRECIP}^c\,\mathrm{RD}^d$	221.58	7.20	0.02
	$y = a\mathrm{DA}^b\,\mathrm{PRECIP}^c\,d\mathrm{RD}^e$	225.39	11.01	0.00
	$y = a\mathrm{DA}^b\,\mathrm{PRECIP}^c\,\mathrm{RFC}^d$	231.94	17.56	0.00
Fine sediment	$y = a + b\mathrm{RD} + c\mathrm{DA} + d\mathrm{PRECIP}$	88.80	0.00	0.19
	$y = a + b\mathrm{TFC} + c\mathrm{DA} + d\mathrm{ALLUV}$	88.85	0.05	0.18
	$y = a + b\mathrm{TFC} + c\mathrm{DA}$	90.49	1.68	0.08
	$y = a + b\mathrm{TFC} + c\mathrm{DA} + d\mathrm{RD}$	90.71	1.91	0.07
	$y = a + b\mathrm{IC} + c\mathrm{DA} + d\mathrm{ELEV}$	90.92	2.11	0.07

Note: RD, road density; IC, impervious cover; TFC, total forest cover; RFC, riparian forest cover; ELEV, elevation; DA, drainage area; GRAD, channel gradient; PRECIP, annual precipitation; ALLUV, alluvium.

Table 8. Models selected to link the four habitat quality attributes with land use characteristics and geomorphic characteristics.

Habitat quality attribute	Parameter	Coefficient	SE	95% CI	
				Lower limit	Upper limit
Prespawning temperature	Constant	14.228	1.128	11.715	16.741
	Riparian forest cover	–0.198	0.032	–0.269	–0.126
	Annual precipitation	0.051	0.010	0.029	0.073
	Alluvium	–0.058	0.025	–0.114	–0.001
Incubation temperature	Constant	7.078	0.397	6.233	7.925
	Road density	0.349	0.131	0.069	0.628
	Elevation	–0.006	0.001	–0.008	–0.004
Peak flow	Constant	2.148×10^{-5}	4.574×10^{-5}	7.547×10^{-5}	1.184×10^{-4}
	Drainage area	0.774	0.029	0.713	0.835
	Annual precipitation	2.124	0.365	1.349	2.898
	Impervious cover	0.040	0.008	0.023	0.057
Fine sediment[a]	Constant	1.387	0.635	0.074	2.700
	Total forest cover	–0.054	0.010	–0.075	–0.032
	Drainage area	0.002	0.001	0.001	0.003
	Alluvium	–0.045	0.022	–0.090	-3.4×10^{-4}

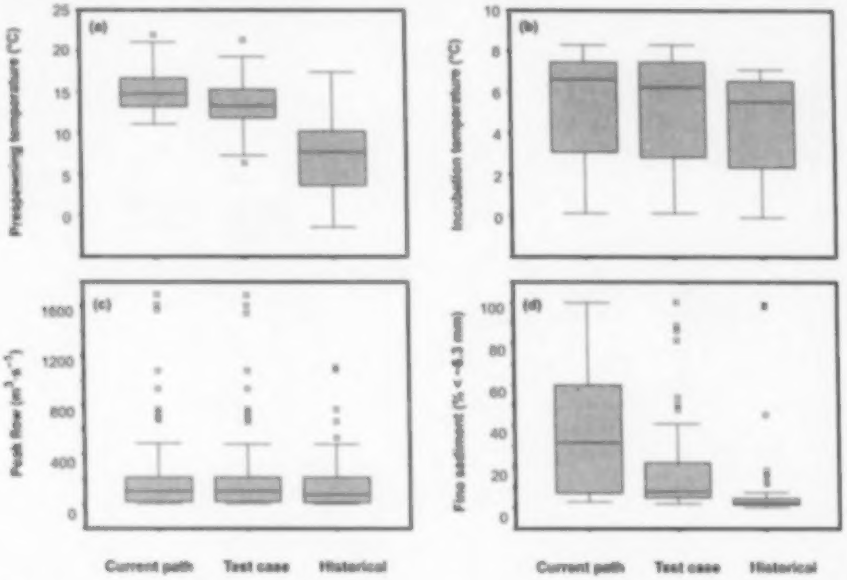
Note: For each coefficient, the standard error (SE) and 95% confidence intervals (CI) are provided. The confidence intervals enable the generation of simulated parameters for the Monte Carlo trials.

[a] Variable is logit transformed.

because three of the four models with $\Delta_i \leq 2$ included total forest cover, lending support for this choice.

We entered the target values from Table 2 into the appropriate statistical models to generate changes in habitat quality under the alternative scenarios. The resulting median stream temperature during the prespawning period was 14.8 °C under the current path, 13.3 °C under the test case, and 7.8 °C under the historical scenario (Fig. 3*a*; $n = 62$ subbasins). Confidence intervals for prespawning temperature ranged from ±0.3 to ±1.0 °C, depending on subbasin (or from ±2% to ±530% if expressed as percentages of the mean). For incubation temperature, the median estimates across subbasins were 6.6, 6.2, and 5.6 °C under the current path, test case, and historical scenarios, respectively (Fig. 3*b*). Confidence intervals within subbasins for the incubation temperature estimates ranged from ±0.1 to ±0.3 °C (or from ±1% to ±299% when expressed

Fig. 3. Box-and-whisker plots of the four habitat quality attributes ((*a*) prespawning temperature, (*b*) incubation temperature, (*c*) peak flow, and (*d*) fine sediment) as estimated under the alternative scenarios. For each box, the midline is the median value (n = 62 subbasins). The lower and upper bounds are the 25th and 75th percentiles, and the lower and upper whiskers are the 10th and 90th percentiles. Squares above and below the whiskers represent outliers.



as percentages of the mean). The median peak flow was 101.3 m^3·s^{-1} under the current path, 101.1 m^3·s^{-1} under the test case, and 75.3 m^3·s^{-1} under the historical scenario (Fig. 3*c*). Confidence intervals in individual subbasins were asymmetrical for peak flow: lower limits ranged from 0.8 to 793.5 m^3·s^{-1} below the mean (or 26%–49% when expressed as percentages of the mean), and upper limits ranged from 1.2 to 1393.9 m^3·s^{-1} above the mean (or 40%–88%). The fine sediment medians were 31.8% and 8.1% for the current path and test case, respectively, and 2.8% for the historical scenario (Fig. 3*d*). As with peak flow, the fine sediment confidence intervals were asymmetrical around the subbasin-scale means from the Monte Carlo trials. Lower limits ranged from < 0.1% to 14.2% below the mean, whereas upper limits ranged from <1% to 13.4% above the mean.

Changes in habitat quantity under the alternative scenarios

Potential juvenile capacity

The potential rearing area under the current path scenario was 21.2 km^2 basin-wide (Fig. 4*a*). The potential rearing area under the test case scenario was 42.4 km^2. Although the test case estimate doubled the current path estimate, it was still 21% less than the historical estimate of 53.9 km^2. These differences resulted primarily from changes in the area of off-channel habitat, which decreased from 35.5 km^2 under the historical scenario to 23.4 km^2 under the test case and 3.0 km^2 under the current path. The decrease in off-channel area was partly offset by an increase in channel area, due to the policy of transporting Chinook salmon above Sunset Falls.

The potential juvenile capacity estimates followed the same pattern as the rearing area estimates in that capacity under the test case was intermediate between the current path and historical estimates (~3 333 000, 4 285 000, and 5 273 000 juveniles basin-wide for the current path, test case, and historical scenarios, respectively; Fig. 4*b*). The 95% confidence intervals for individual subbasins were asymmetrical around the means from the Monte Carlo simulations of capacity. Lower limits ranged from 23 to 31 665 juveniles less than the mean (or 2.0%–4.6% when expressed as a percentage of the mean); upper limits ranged from 25 to 33 206 juveniles greater than the mean (or 2.0%–4.9%). Although large mainstem reaches accounted for the greatest proportion of capacity in the basin, off-channel and estuarine habitats primarily determined the differences in capacity among scenarios.

Potential adult capacity

The estimated amount of potential spawning habitat was higher under the current path and test case scenarios than under the historical scenario basin-wide (Fig. 5*a*). This difference, due to the transport of salmon above Sunset Falls, was evident whether spawning habitat was estimated in terms of area or length. For example, spawning area under the future scenarios (current path and test case) was 9.6 km^2, whereas under the historical scenario, it was 7.7 km^2. Similarly, spawning length under the future scenarios was 240.2 km for low-gradient reaches (<1%) and 116.1 km for mid-gradient reaches (1%–4%); under the historical scenario, these estimates decreased to 222.9 and 82.3 km, respectively.

The potential capacity estimates reversed this pattern in that the current path and test case capacities were lower than the historical capacity basin-wide (Fig. 5*b*). Specifically, capacity under the future scenarios was estimated as 98 275

Fig. 4. Potential juvenile (*a*) rearing area and (*b*) capacity, as estimated under each scenario basin-wide. Rearing area and capacity are divided into six habitat types.

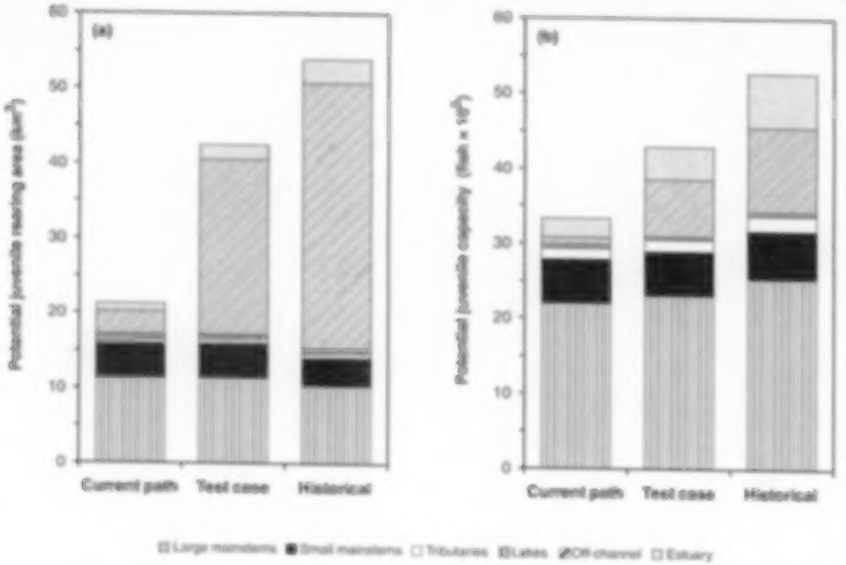
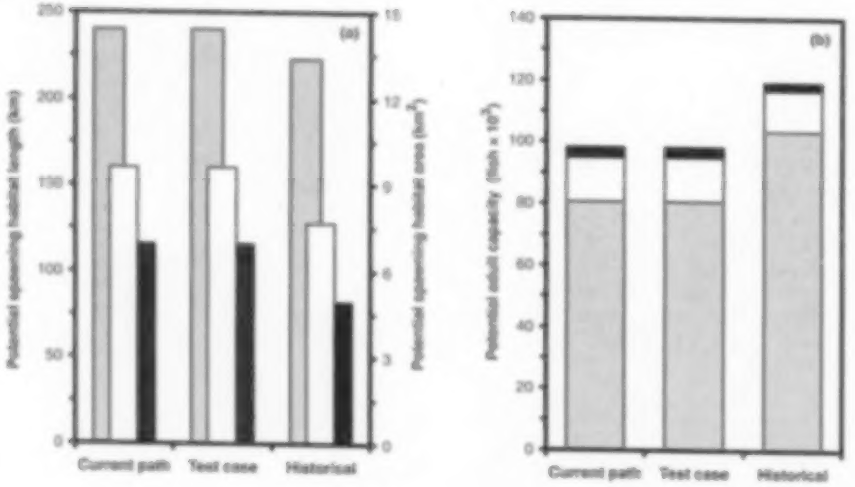


Fig. 5. Potential adult (*a*) spawning habitat and (*b*) capacity, as estimated under each scenario for the entire basin. Habitat is expressed as area for reaches with bankfull widths > 25 m (open bars) and as length for reaches with bankfull widths of 5–25 m (shaded bars, gradient <1%; solid bars, gradient 1%–4%).

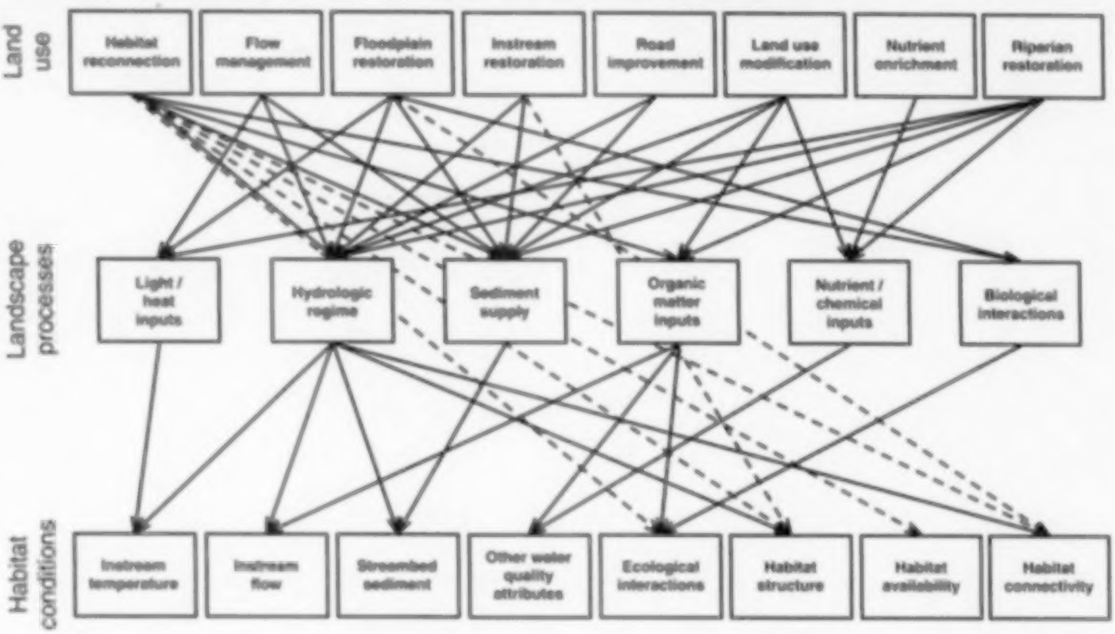


spawners; under the historical scenario, it was estimated as 119 220 spawners. Lower limits for the confidence intervals ranged from 1 to 1553 spawners below the subbasin-scale means (or 5%–11% when expressed as percentages of the mean). Upper limits ranged from 1 to 1631 spawners above the means (or 6%–12%).

Discussion

A crucial step in species conservation planning is to identify the quality, quantity, and distribution of habitat needed by a species for recovery. In most cases, species of conservation concern face many relatively small-scale habitat problems, the cumulative effects of which are significant. It is therefore difficult to determine the best suite of actions for recovering species, especially in cases where several combinations of recovery strategies may work. In instances where empirical information on the integrative effects of recovery actions is scarce, exploring the consequences of alternative actions on species status is a fruitful way to sort through possible strategies. In the example presented here, we translated three alternative scenarios into their likely effects on salmon habitat conditions. Based on available data in the Snohomish basin, we found considerable potential to

Fig. 6. Conceptual diagram of the complex relationships linking land use actions, landscape processes, and salmon habitat conditions. Broken arrows represent direct links between land use actions and salmon habitat conditions.


Land use
Habitat reconnection
Flow management
Floodplain restoration
Instream restoration
Road improvement
Land use modification
Nutrient enrichment
Riparian restoration
Landscape processes
Light / heat inputs
Hydrologic regime
Sediment supply
Organic matter inputs
Nutrient / chemical inputs
Biological interactions
Habitat conditions
Instream temperature
Instream flow
Streambed sediment
Other water quality attributes
Ecological interactions
Habitat structure
Habitat availability
Habitat connectivity

improve both the quality and quantity of habitat under the alternative scenarios.

If the current path and historical medians are viewed as endpoints, improvements in habitat quality could be as large as a 7.0 °C decrease in prespawning temperature, a 1.1 °C decrease in incubation temperature, a 26.0 $m^3 \cdot s^{-1}$ reduction in peak flow, and a 29.0% reduction in fine sediment content. Similarly, improvements in habitat quantity, expressed as increases in juvenile and adult capacity, could be as large as 1 940 000 juveniles and 21 000 adults basin-wide. Although we account for uncertainty in our subbasin-scale estimates, we do not provide confidence intervals for these potential basin-scale improvements because habitat quality and quantity vary widely from the headwaters to the delta in the basin, regardless of modeling error. In the absence of basin-wide confidence intervals, the true value of these estimates may be in allowing managers to explore relative comparisons in habitat change among the alternative scenarios.

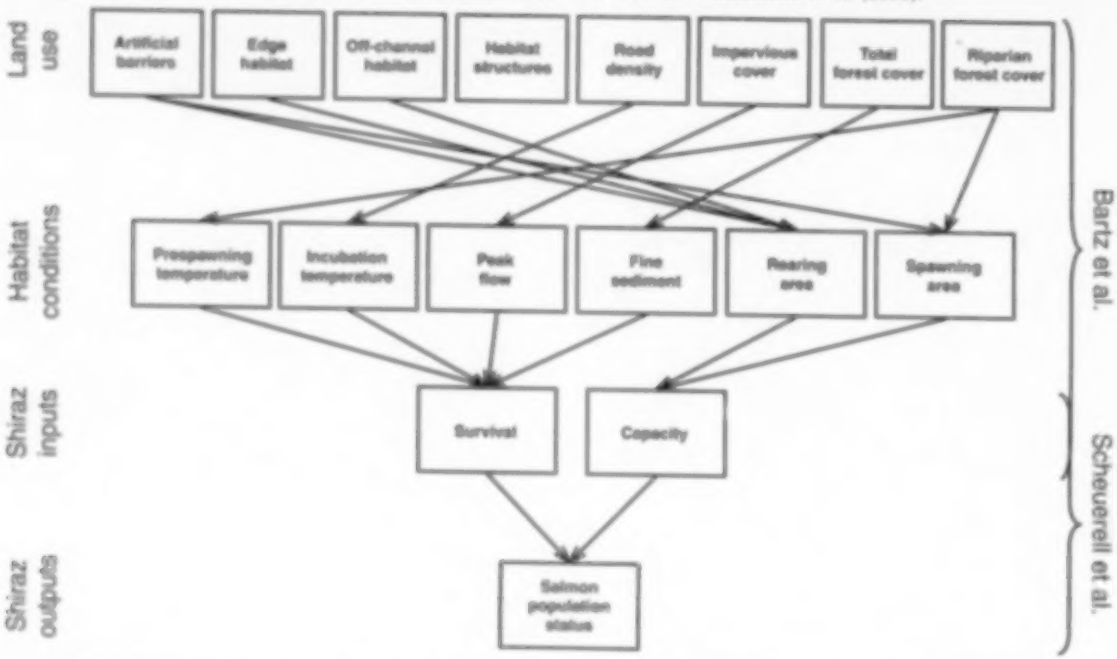
Many studies have linked land use actions and salmon habitat conditions at small scales, and several studies have used alternative scenarios to link habitat conditions with salmon population status (e.g., McHugh et al. 2004; Sharma et al. 2005). However, few studies have made both links at scales relevant to salmon recovery planning. Even in the broader literature, few studies that we know of have undertaken both of these analytical steps explicitly, although several have established connections between either land use or habitat and some indicators of species status (e.g., spotted owls (*Strix occidentalis caurina*), Lee and Irwin 2005; grizzly bears (*Ursus arctos horribilis*), Linke et al. 2005; butterflies, Schultz and Crone 2005). For these reasons, the approaches documented here and in Scheuerell et al. (2006) may provide conservation planners with an improved framework for choosing and defending recovery strategies.

Habitat quality

Mechanistic models have been created to predict habitat quality attributes, including SNTEMP for predicting temperature (Theurer et al. 1984), DHSVM for predicting flow (Wigmosta et al. 1994), and HEC-6 for predicting sediment deposition (US Army Corps of Engineers 1977). Our reasons for developing statistically based models, rather than using the existing mechanistic models, are pragmatic. First, most of the mechanistic models are exceedingly data and computation intensive at the basin scale. Second, the inputs of the mechanistic models are not entirely equivalent to the land use data in Table 2, and the outputs are not always consistent with the habitat data required by Shiraz (Scheuerell et al. 2006). We currently are using DHSVM in the Snohomish basin to estimate shifts in stream flow due to land use and climate change. Preliminary results indicate a strong correlation between the flow estimates reported here and those generated through DHSVM ($r = 0.98$, $p < 0.01$, $n = 53$ subbasins; J. Battin, Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Boulevard East, Seattle, WA 98112, USA, unpublished data).

Further validation of our statistical models is challenging, given the lack of empirical historical data and the scarcity of current data not used during model development. For the incubation temperature and fine sediment models, all available current data were used for model development. For the prespawning temperature and peak flow models, some gages

Fig. 7. Mechanistic diagram of the linkages estimated in this analysis and in that of Scheuerell et al. (2006).



were omitted from the initial data set and thus could be used for validation purposes. We conducted validation analyses by comparing the observed value at a gage with the predicted value for the subbasin where that gage was located. The outcome for prespawning temperature ranged from a modest correlation ($r = 0.67$, $p = 0.01$, $n = 13$) to a weak correlation ($r = 0.16$, $p = 0.60$, $n = 13$), depending on which gage of several per subbasin was included in the analysis. The correlation between observed and predicted peak flows was strong ($r = 0.99$, $p < 0.01$, $n = 7$), regardless of the choice of gage.

Habitat quantity

The potential juvenile capacity estimates are generated by multiplying rearing areas and juvenile densities in different habitat types. The juvenile densities are constant across scenarios, so differences in capacity among scenarios are attributable solely to changes in rearing area. Changes in area are limited to three types of habitat: channel, off-channel, and estuarine. The area of off-channel habitat differs more among scenarios than the areas of channel or estuarine habitats. However, juvenile densities in off-channel habitats (on average, 0.04 Chinook $\text{salmon}\cdot\text{m}^{-2}$) are nearly an order of magnitude lower than densities in the other habitats (on average, 0.30 and 0.23 Chinook $\text{salmon}\cdot\text{m}^{-2}$ in channel habitats and estuarine habitats, respectively), and this is evident in the small contribution of off-channel habitat to basin-wide capacity, relative to basin-wide rearing area, within a given scenario.

The juvenile densities in our analysis originate from a limited number of observed values in the literature. These values are likely to be low-end estimates as salmon populations in the Pacific Northwest are depressed relative to historical levels (Ruckelshaus et al. 2002). As a result, our estimate of historical potential capacity for juveniles is probably lower than the true value, indicating that Snohomish salmon populations may have suffered more severe declines in juvenile production than our results suggest.

We estimate that more spawning habitat is available under the future scenarios than under the historical scenario. Conversely, potential adult capacity is greater under the historical scenario than under the future scenarios according to our estimates. This difference in adult capacity among scenarios is driven by large mainstem reaches with gradients ≤4%, specifically by their increase in the percentage of spawnable habitat from 6.2% to 9.7%. Because 9.7% is simply the highest of the available current measurements, it may underestimate the true historical percentage. Historical adult capacity, therefore, may be underestimated as well.

Remaining questions

As is almost always the case for salmon recovery efforts, local data in the basin are insufficient to allow us to estimate all the conceivable linkages between land use actions, landscape processes, and salmon habitat conditions (Fig. 6). Rather than relying on expert opinion, we limit the scope of our analysis mainly to those linkages that we can estimate with local data alone (Fig. 7). As a result, many potential effects on habitat of the land use actions proposed by the SBSRTC are not quantified in our analysis. This suggests that we are likely underestimating the overall effects of the alternative scenarios on salmon habitat conditions.

We do not represent interactions among land use actions or the effects of those interactions on salmon habitat conditions. We also do not attempt to quantify the ancillary benefits to other species of restoring landscape processes. Furthermore, our approach generates a snapshot of habitat conditions that could result from alternative land uses in the basin. It does not capture how temporal variability in these conditions might be altered by the alternative scenarios, nor does it capture the multiple trajectories that might occur when impacted subbasins are restored. Each of these limitations could contribute to the uncertainty in our estimates of habitat conditions.

Supporting conservation decisions in the face of uncertainty

The question facing conservation planners in the Snohomish basin is one that challenges managers of any imperiled plant or animal: which suite of actions aimed at protecting and restoring habitat will result in recovery of the species? For most species, this is a complex question, given the biological and physical interactions driving the habitat conditions that affect species status. For wide-ranging species such as salmon, which have life cycles spanning freshwater, estuarine, nearshore, and open ocean environments, the challenge is even greater. Scientists can help planners and managers face such a challenge by (*i*) developing quantitative models with clearly documented assumptions, (*ii*) comparing the relative habitat and species responses to alternative strategies, and (*iii*) presenting the results as distributions to indicate the degree of certainty.

In this example, we have tried to cover each of these points. However, the complexity of the biological system for which we generated estimates, and the difficulties with validating more than individual components of those estimates, mean that monitoring changes in habitat conditions will be important once a conservation strategy is implemented. True validation of the estimates will become possible as basin-wide data are collected. In the meantime, the SBSRTC is designing an adaptive management program to further test assumptions and to make adjustments in the strategy as needed.

Although our approach is likely to underestimate the overall effects of restoration scenarios on salmon and other aquatic species, results indicate that there is considerable potential to improve salmon habitat in the Snohomish basin. This is encouraging, given the uncertainty inherent in predicting the cumulative effects of land use on habitat conditions (Pess et al. 2003). The ultimate question that salmon recovery planners and conservation planners in general must address is how a conservation strategy will affect the population status of imperiled species. This paper represents the first step in answering that question. How such improvements in habitat affect salmon population status is the subject of the following paper (Scheuerell et al. 2006).

Acknowledgments

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The Shiraz model: a tool for incorporating anthropogenic effects and fish–habitat relationships in conservation planning

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Abstract: Current efforts to conserve Pacific salmon (*Oncorhynchus* spp.) rely on a variety of information sources, including empirical observations, expert opinion, and models. Here we outline a framework for incorporating detailed information on density-dependent population growth, habitat attributes, hatchery operations, and harvest management into conservation planning in a time-varying, spatially explicit manner. We rely on a multistage Beverton–Holt model to describe the production of salmon from one life stage to the next. We use information from the literature to construct relationships between the physical environment and the necessary productivity and capacity parameters for the model. As an example of how policy makers can use the model in recovery planning, we applied the model to a threatened population of Chinook salmon (*Oncorhynchus tshawytscha*) in the Snohomish River basin in Puget Sound, Washington, USA. By incorporating additional data on hatchery operations and harvest management for Snohomish River basin stocks, we show how proposed actions to improve physical habitat throughout the basin translate into projected improvements in four important population attributes: abundance, productivity, spatial structure, and life-history diversity. We also describe how to adapt the model to a variety of other management applications.

Résumé : Les efforts actuels pour la conservation des saumons du Pacifique (*Oncorhynchus* spp.) se basent sur une variété de sources d'information, dont les observations empiriques, les opinions d'experts et les modèles. Nous élaborons ici un cadre pour incorporer dans la planification de la conservation, de façon variable dans le temps et explicite dans l'espace, des données détaillées sur la croissance de population dépendante de la densité, sur les caractéristiques de l'habitat, sur les opérations de pisciculture et sur la gestion de la récolte. Nous utilisons un modèle de Beverton–Holt à plusieurs niveaux pour décrire la production de saumons d'un stade à l'autre de leur cycle. Des renseignements tirés de la littérature nous servent à établir les relations entre l'environnement physique et les paramètres de productivité et de capacité requis par le modèle. Comme exemple de l'utilisation possible du modèle pour la planification de la récupération par des responsables des politiques de gestion, nous appliquons notre modèle à une population menacée de saumons chinook (*Oncorhynchus tshawytscha*) du bassin de la Snohomish dans le Puget Sound, Washington, É.-U. En incorporant des données additionnelles sur les opérations de pisciculture et sur la gestion de la récolte pour les stocks du bassin de la Snohomish, nous montrons comment les actions prévues pour améliorer l'habitat physique dans l'ensemble du bassin résultent en des améliorations anticipées de quatre caractéristiques démographiques importantes, soit l'abondance, la productivité, la structure spatiale et la diversité des cycles biologiques. Nous décrivons aussi comment adapter le modèle à une gamme d'autres usages de gestion.

[Traduit par la Rédaction]

Introduction

Salmon populations throughout the Pacific Northwest have declined dramatically over the past century owing to a variety of anthropogenic impacts and changes in climate (National Research Council 1996; Ruckelshaus et al. 2002). A necessary step in developing salmon recovery plans involves estimating the relative effects of habitat degradation, hatchery operations, harvest management, and hydropower dams (i.e., "the four Hs"), as well as interactions with other species and other environmental factors on salmon population status (Ruckelshaus et al. 2002). This task is often difficult when

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dealing with salmon, however, because of the variety of freshwater, estuarine, and marine habitats that they occupy during their diverse life history (Mobrand et al. 1997; Greene and Beechie 2004; Sharma et al. 2005). Population models offer a useful way of integrating the effects of the four Hs on salmon populations, particularly models that incorporate these effects on life-stage-specific survival or capacity. Nonetheless, most models provide population viability analyses to estimate population growth rates and threat of extinction (e.g., Kareiva et al. 2000; Ellner and Fieberg 2003; Wilson 2003) without any specific allowances for density-dependent dynamics caused by the direct interaction between habitat conditions and fish population performance (Greene and Beechie 2004; Zabel et al. 2006).

Modeling fish–habitat relationships is not a new endeavor. For salmon in particular, a rich literature exists describing how changes in the quantity and quality of habitat affect the survival of various life stages (e.g., Tappel and Bjorn 1983; Chapman 1988; Kondolf 2000). Although some studies have modeled the influence of in-stream habitat attributes on the survival of salmon at specific life stages (e.g., Lisle and Lewis 1992; McHugh et al. 2004), only recently have researchers done so across the entire life cycle, demonstrating the importance of various habitat changes on the overall population dynamics of salmon (see Nickelson and Lawson 1998; Greene and Beechie 2004; Sharma et al. 2005). Additionally, changes in land use by humans will continue to affect salmon populations through their indirect effects on habitat-forming processes (Beechie and Bolton 1999; Regetz 2003). Predicting the impacts of current and future alterations to salmon habitat requires a holistic modeling perspective that captures not only the expected future population size, but also detailed information on stock productivity, spatial structure, and the diversity of life-history types (Lichatowich et al. 1995; Mobrand et al. 1997; McElhany et al. 2000).

Here we outline a framework for incorporating the effects of habitat change, hatchery operations, and harvest management actions on salmon population status for use in recovery planning. The Shiraz model utilizes a set of user-defined relationships among habitat attributes, fish survival, and carrying capacity to evaluate population performance across space and time. The model allows us to translate the effects of changes in habitat conditions resulting from land-use restoration and protection actions into consequences for salmon population status and likelihood of recovery. Furthermore, the Shiraz model provides estimates of the four important criteria for describing viable salmon populations (VSP): abundance, productivity, spatial structure, and diversity (McElhany et al. 2000). We illustrate our model framework using available data from the Snohomish River basin, which contains two of the 22 remaining populations of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound listed as threatened under the Endangered Species Act (National Marine Fisheries Service 1999). A multi-stakeholder recovery planning group in the Snohomish River basin has adopted population-specific salmon recovery targets to describe salmon population attributes necessary for viability. In collaboration with them, we evaluated the potential consequences of habitat conservation alternatives (Bartz et al. 2006) for salmon population status using the Shiraz model. Our analyses subsequently helped the policy group refine their conservation alternatives and select a preferred recovery plan based on the predicted outcomes for the two Chinook salmon populations in their basin.

Materials and methods

Study area and species

The Snohomish River basin is located north and east of Seattle, Washington, USA (Fig. 1), and the river's estuary runs adjacent to Everett, Washington. Agricultural, urban, and suburban land use dominate the lower (western) region of the watershed, whereas forests largely cover the upper (eastern) region that extends to the crest of the Cascade Mountains. The two Chinook populations in the basin generally return to the river in the summer and spawn in the fall (Ruckelshaus et al. 2006). Most juveniles migrate as subyearlings, spending some time rearing in the Snohomish River estuary before continuing into the Pacific Ocean, but a small fraction of juveniles rear for a year in the stream and migrate as yearlings. Two hatchery facilities in the basin rear three distinct stocks of Chinook salmon (see Hatchery operations below). Other salmonid species in the basin include coho (*O. kisutch*), pink (*O. gorbuscha*), and chum (*O. keta*) salmon and bull trout (*Salmo confluentus*).

Fish stocks and life history within the modeling framework

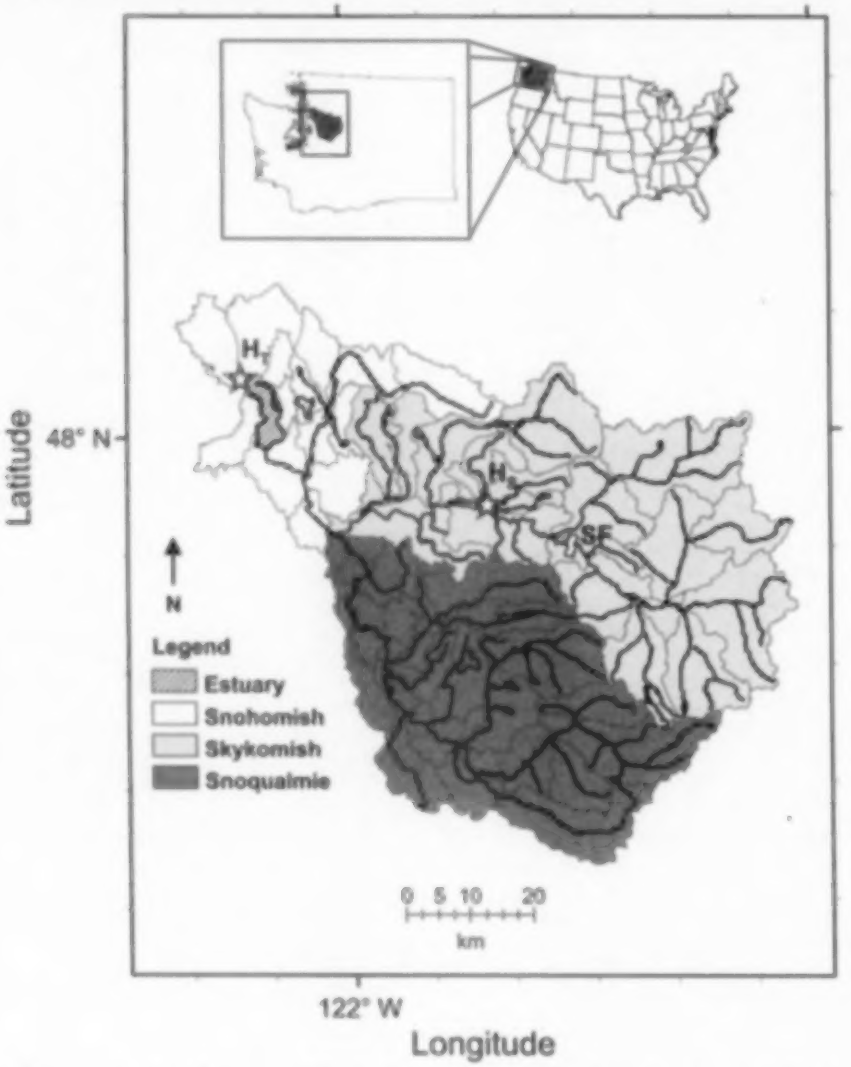
The Shiraz model framework (Fig. 2) begins by assigning fish to various "stocks" that might represent (*i*) different life-history types (e.g., ocean-type vs. stream-type Chinook), (*ii*) different origin (e.g., wild or hatchery fish), or (*iii*) different species. Coincident with assigning fish to their respective stocks, one must specify each life-history trajectory, a description of the habitat types that an individual traverses throughout its life cycle and the time spent in each. This could take the simple case of only considering spawners and their subsequent offspring that recruit back to freshwater, or it could assume a much more detailed form. In the Snohomish case study, we used the following life-history stages: mature adults returning from the ocean to rivers, spawning adults that survived harvest, eggs, fry, smolts, and ocean ages 1–5. We considered only ocean-type Chinook salmon that go to sea after only a few months of rearing in freshwater habitat (Healey 1991).

We assigned wild and hatchery fish to different stocks, which allowed us to track separate changes in their survival due to varying environmental effects or harvest policies. It also enabled us to investigate the impact of various hatchery operations on overall stock performance. Another important concept in the Shiraz model is stock transformation, such that at the time of spawning, individuals from one stock can change their stock identity. For example, the progeny of hatchery fish that stray and naturally spawn are considered wild fish in the next model generation. Another possible application might include a life-history type that depends on estuarine rearing whereby a small fraction (maybe 5%) of nonestuarine-rearing fish transform into estuarine-rearing fish.

Spatial resolution

As the model is spatially explicit, the user must decide what level of spatial resolution to consider. Explicitly modeled spatial units could be as broad as an entire watershed or

Fig. 1. Map of the Snohomish River basin (Washington, USA) showing the primary reaches of the Snoqualmie, Skykomish, and Snohomish rivers (thick black lines) and the 62 subbasins (thin black lines). Also shown are the locations of the tribal (H_T) and state (H_S) salmon hatcheries (stars) and Sunset Falls (SF), a natural barrier to anadromous fish.



as fine as individual stream reaches, but once defined, the model assumes that all spatial units are identical in size with respect to fish movement (see below). The Shiraz model tracks fish during their freshwater residency and seaward migration within each unit, and subsequent spawners return to their natal locations to spawn unless they stray. For this case study, we used the 62 subbasins within the Snohomish River watershed (including the estuary) as our level of spatial resolution (Fig. 2). These subbasins ranged in size from 12.2 to 246 km^2, and the total length of stream within each subbasin ranged from 0.34 to 98 km. We treated the estuary and ocean as one "subbasin" each because of the relatively large spatial scales over which fish use them and the limited survival data with which to parameterize the model. The model is structured such that another application could split freshwater, estuarine, and marine habitats into a variety of spatial units, depending on available data and user preferences.

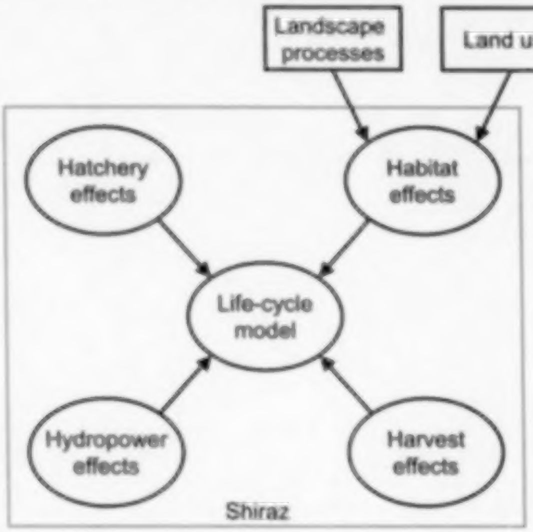
Temporal resolution

The model generally operates on an annual time scale but considers that several life-stage transitions might occur within a given year (e.g., spawning of eggs and the emergence of the fry from the gravel). This allows fish of different species, stocks, or life-history stages to interact with one another in the various spatial units. By defining a beginning and an end year, the model allows for forward projections of population size by stock, life stage, and location.

Habitat indicators

We use the underlying physical environment as the primary driver of fish population dynamics. Therefore, the user must

Fig. 2. Conceptual diagram of the Shiraz model framework indicating how various anthropogenic impacts (four Hs) can be used to drive biological responses of fish through a life-cycle model. The influence of human land use and natural landscape processes on habitat attributes is treated in Bartz et al. (2006).



specify a set of habitat indicators that potentially affect fish population status for each area of interest. These can be detailed physical factors such as stream gradient or width, percentage of pools, riparian vegetation cover, or habitat quantities such as juvenile rearing area, spawning area, etc. Habitat indicators can change over time gradually by exponential or logistic growth (or decay) but do not change from year to year in a stochastic way in this model. For those kinds of inputs (e.g., stream flow or temperature), the user must define stochastic variables as described below. For our case study, we relied on physical habitat indicators for estimating the capacity of juvenile and adult salmon and for predicting prespawning mortality and the survival of eggs to fry because of availability of data and functional relationships (see Bartz et al. 2006).

Stochastic variables

The Shiraz model uses two methods for addressing uncertainty in model inputs. The first approach requires the user to specify parameters for any of three statistical distributions (uniform, normal, lognormal) from which the model will draw random variates at each time step. Variates then replace the otherwise constant parameter values in the functional relationships or the static estimates of habitat condition used in the functional relationships (Appendix A). Because variability tends to be highly correlated across space, the normal method is to draw one random variate for each major section of a watershed per time step and tie survival rates to this variate over most, if not all, areas. Second, one can estimate the overall effect of stochastic variables by using a Monte Carlo approach whereby the model is run a specified number of times while drawing random variates. Model output (e.g., the number of spawners by area) is evaluated at some time point during each Monte Carlo simulation, typically at the end of a prespecified number of years. At the end of all simulations, summary statistics such as the mean and variance are computed for the output variables of interest. This approach is useful for evaluating the effects of various harvest management strategies, hatchery operations, or changes in ocean conditions.

Initial conditions

In addition to habitat values, functional relationships, and movement criteria specified below, the Shiraz model requires the user to set other initial conditions for a model run. This includes specifying how many individuals of each life stage and stock are alive and the proportion of each life stage occupying each geographical area. At a minimum, one must designate the initial number and spatial distribution of spawners so that the model can track subsequent life stages through space and time. However, one could also specify an entire age distribution across all life stages.

The model scenarios

We modeled three different scenarios to reflect our best estimates of the differences in physical habitat under pre-European settlement conditions (historical), present land use and management and policies (current path), and proposed future policies (test case). The Snohomish Basin Salmonid Recovery Technical Committee developed a set of management actions that consisted of restoring riparian habitat, removing dikes and revetments, decommissioning roads, etc. We transformed their set of potential actions under the test case into changes in physical habitat (see Bartz et al. 2006) and used them as inputs into the Shiraz model to evaluate the potential population response of Chinook salmon within the basin. We also assumed that hatchery operations and harvest rates would continue as implemented under the current path and therefore did not make any adjustments under the test case.

Model formulation

The model development begins with a multistage Beverton–Holt model (Moussalli and Hilborn 1986):

$$(1)\qquad N_{s+1} = \frac{N_s}{\dfrac{1}{p_{s\to s+1}} + \dfrac{1}{c_{s+1}} N_s}$$

where the number of fish surviving to their next life-history stage (N_{s+1}) is a function of the number alive at the current life stage (N_s), their survival or productivity to the next stage ($p_{s\to s+1}$), and the capacity of the environment to support them (c_{s+1}). The parameters p and c can assume fixed values or be functions of the environment (see below). Furthermore, at each life stage, p and c can be a single-point estimate or the product of several estimates, such that

$$(2)\qquad p_{s\to s+1} = \prod_r p_{s\to s+1,r}$$

$$(3)\qquad c_{s\to s+1} = \prod_r c_{s\to s+1,r}$$

where r represents the number of functional relationships for a given life stage. The basic habitat model consists of specifying how habitat indicators and stochastic variables relate to productivity and survival. A range of functional forms is avail-

Table 1. The parameter values and functional relationships affecting the productivity (survival) and capacity of each life stage for the Shiraz application to the Snohomish River basin.

Life-stage transition	Productivity (p)	Life stage	Capacity (c)
Spawners[a] to eggs	f_1(temperature)[b]	Eggs	2500·c_1(habitat)[c]
Eggs to fry	f_2(temperature, flow, sediment)[d]	Fry	c_2(habitat)[e]
Fry to smolt	0.332	Smolts	c_3(habitat)[f]
Smolts to 1-ocean	0.033	1-ocean	∞
1-ocean to 2-ocean	0.6	2-ocean	∞
2-ocean to 3-ocean	0.7	3-ocean	∞
3-ocean to 4-ocean	0.8	4-ocean	∞

Note: Unless otherwise noted, parameter values come from Greene and Beechie (2004). See Materials and methods section for details regarding the forms of the functional relationships.

[a] Spawners are first converted to potential eggs (eq. 18) before applying eq. 1.

[b] Prespawning mortality is a nonlinear function of temperature (Cramer 2001).

[c] The egg capacity equals an index of spawner fecundity (5000 eggs per female), divided by 2 to account for females only, times the estimated spawner capacity from B. Sanderson (Northwest Fisheries Science Center, 2725 Montlake Boulevard E., Seattle, WA 98112, USA, unpublished data). See Bartz et al. (2006) for details.

[d] Egg-to-fry survival is a nonlinear function of temperature (Velsen 1987; Beacham and Murray 1989), river flows (Seiler et al. 2003), and fine sediment (Tappel and Bjorn 1983).

[e] Fry capacity is derived from the detailed habitat analyses described in Bartz et al. (2006).

[f] Smolt capacity is derived from the detailed habitat analyses described in Bartz et al. (2006).

able to develop these relationships, including simple linear, exponential, and line segments (Appendix A).

Functional relationships

For our case study, we used habitat-based functions to relate various attributes of the physical environment to the productivity (survival) and capacity of several life stages. For survival, these included the transitions from spawners to eggs and from eggs to fry. For capacity, these included eggs, fry, and smolts. These functional relationships vary across space but we omit the area subscripts below for simplicity. First, we modeled the prespawning survival of adults in the river (p_1) as a nonlinear function of water temperature (T_{pre}, in °C) during a portion of the spawning period (15 July through 15 August), based on the analyses of Cramer (2001), such that

$$(4)\qquad p_1 = \begin{cases} 1 & \text{if } T_{\mathrm{pre}} < 16 \\ 1 - 0.15(T_{\mathrm{pre}} - 16) & \text{if } 16 \le T_{\mathrm{pre}} < 22.6 \\ 0.01 & \text{if } T_{\mathrm{pre}} \ge 22.6 \end{cases}$$

We used three separate relationships for estimating the effects of the physical environment on egg-to-fry survival. The first, a nonlinear function ($p_{2,1}$) of water temperature (T_{inc}) during the incubation period (15 September through 15 February), is a series of line segments fit from data in Velsen (1987) and Beacham and Murray (1989), where

$$(5)\qquad p_{2,1} = \begin{cases} 0.273T_{\mathrm{inc}} - 0.342 & \text{if } 1.3 \le T_{\mathrm{inc}} < 4.7 \\ 0.94 & \text{if } 4.7 \le T_{\mathrm{inc}} < 14.3 \\ -0.245T_{\mathrm{inc}} + 4.44 & \text{if } 14.3 \le T_{\mathrm{inc}} < 18.1 \\ 0.01 & \text{if } T_{\mathrm{inc}} \ge 18.1 \end{cases}$$

Second, we modeled egg-to-fry survival as a linear function ($p_{2,2}$) of the normalized mean flow during the incubation period (Q^*). To do so, we mapped the maximum daily mean flow during the incubation period (Q) onto the interval [0,1] by dividing it by the maximum flow ($Q_{\max}$) for a 100-year period as predicted by Sumioka et al. (1998). Seiler et al. (2003) presented a flow–survival relationship across the egg-to-smolt stages, but we wanted it for the egg-to-fry stage only. Therefore, we assumed that the entire flow effect manifested itself during the egg-to-fry transition and divided all of Seiler and colleagues' survival estimates by the fry-to-smolt survival (p_3 = 0.332) reported by Greene and Beechie (2004). We then fit the following relationship between our newly estimated egg-to-fry survival and normalized flow (Q^*):

$$(6)\qquad p_{2,2} = \begin{cases} 0.58 - 0.844Q^* & \text{if } Q^* < 0.675 \\ 0.01 & \text{if } Q^* \ge 0.675 \end{cases}$$

Lastly, egg-to-fry survival was also modeled as a nonlinear function of the percent fine sediment (<6.3 mm) in the spawning gravel ($p_{2,3}$). Based on data from Tappel and Bjornn (1983), we developed the following relationship between egg-to-fry survival and the proportion of fine sediment (f)

$$(7)\qquad p_{2,3} = \begin{cases} 0.95 & \text{if } f < 0.268 \\ -3.32f + 1.81 & \text{if } 0.268 \le f < 0.544 \\ 0.06 & \text{if } f \ge 0.544 \end{cases}$$

We then combined the three terms for egg-to-fry survival according to eq. 2. For the remaining productivity and capacity parameters necessary for describing the complete life cycle, we used either point estimates from the literature or model-driven values (Table 1).

Hatchery operations

The model simulates hatchery operations from two perspectives: the number of eggs taken from returning spawners and the number of juveniles released back into the river. The user specifies the number of eggs to take each year and the stock from which they are to be taken. After accounting for hatchery mortality as a result of egg takes, any remaining fish may be allowed to spawn in the wild. For hatchery releases, the user must specify the life stage(s) of fish (e.g., subyearlings, yearlings), the number of fish of each stage to release, and the location within the watershed where the fish should be released. After release, hatchery fish follow survival and capacity rules, whether similar to or different from, those applied to the wild fish. Any returning adults are also subject to harvest as described below.

The Snohomish River basin has two operating hatcheries with Chinook salmon programs: the Tulalip Tribe's Bernie Kai-Kai Gobin Hatchery directly north of the estuary on Tulalip Bay and the Washington Department of Fish and Wildlife's (WDFW) Wallace River Hatchery much farther upstream (Fig. 2). We modeled hatchery releases according to the current schedules used by both hatchery management programs (Table 2). The Bernie Kai-Kai Gobin Hatchery releases juveniles from two different fish stocks at the subyearling stage immediately upstream of Tulalip Bay in Puget Sound. These fish interact with wild fish and other hatchery stocks in the estuary and nearshore areas. The Wallace River Hatchery releases fish from one stock at two different ages, subyearling and yearling; both size classes migrate to the estuary shortly after their release from the hatchery and interact with any wild fish along the way.

Table 2. The name, stocks, release life stage (age), and targeted release numbers for the two hatcheries operating within the Snohomish River basin.

Hatchery name	Fish stock	Life stage	Annual releases
Bernie Kai-Kai Gobin	Summer	Fingerling	1 500 000
	Fall	Fingerling	200 000
Wallace River	Summer	Fingerling	1 000 000
	Summer	Yearling	250 000

Fish movement

Within the model, fish can move between areas, and once movement takes place, Shiraz tracks the number of fish by life stage, stock, year, area of birth, and current area of residence. The model directs adult fish (with specified stray rates) to return to their natal areas when spawning takes place while allowing for movement at any number of life-history stages. This movement can be specified either by a fixed preference (i.e., the proportion of fish moving from area *i* to area *j*) or by letting the fish migrate to an area based on their expected survival in that area according to an ideal free distribution (IFD; sensu Fretwell 1972). For each freshwater life stage *s* and stock *k* where movement occurs, the user must specify a matrix of constant movement probabilities ($\mathbf{M}_{s,k}$), which should represent the physical structure of the watershed and realistic downstream migration patterns. In our case, the probability of moving from one area to another is independent of the actual size of the area. For IFD movement, the expected "fitness" (ϕ) for a stage *s* of stock *k* in an area *i* is

$$(8)\qquad \phi_{s,k,i} = \frac{1}{\left(\frac{1}{p_{s,k,i}} + \frac{N_{s,i}}{c_{s,k,i}}\right)}$$

where *N* is the total number of fish and *p* and *c* are the productivity (survival) and capacity, respectively. The idea is that fish "sample" the environment during their early life stages and then move to maximize fitness for all fish. Furthermore, we provide a parameter μ for a "mixed" solution, so that the spatial allocation can be weighted by the intrinsic movement probability and by trying to maximize survival, where

$$(9)\qquad \pi_{s,k,i\to j} = \left(M_{s,k,i\to j}\right)^{\mu} \cdot \left(\frac{\phi_{s,k,i}}{\phi_{s,k,\max}}\right)^{(1-\mu)}$$

and $\phi_{s,k,\max}$ is the maximum fitness across all areas for a given life stage and stock. The number of fish after movement (*N*) in an area *j* is then

$$(10)\qquad N_{s,k,j} = \pi_{s,k,i\to j} N_{s,k,j}$$

In our example, we chose to let fry move downstream according to a specified movement matrix without any specific knowledge of the quality of the habitat (i.e., μ = 1). In this case, juveniles fill up their natal habitat first and then migrate downstream to the next available subbasin without moving upstream again (i.e., no rheotaxis). This is analogous to an ideal free distribution for a territorial organism, usually referred to as an "ideal despotic distribution" (Fretwell 1972; Tregenza and Thompson 1998). We adopted this latter approach because we are unaware of any evidence of salmon following IFD movement rules.

When returning to freshwater habitat to spawn, anadromous salmonids generally exhibit strong homing tendencies for their natal sites, but we know that some level of straying exists (Groot and Margolis 1991). Therefore, the model allows the user to input straying rates from one area to another by stock. When combined with stock transformations, this useful construct can mimic the observed contribution of hatchery-origin fish to the natural spawning population. We applied the observed straying rates of hatchery fish to natural spawning grounds estimated from recoveries of otoliths on the spawning grounds that were thermally marked in the hatchery, thereby distinguishing the fish as hatchery origin (Rawson et al. 2001). Based on otolith recovery data, we assumed that only 3% and 1% of Tulalip hatchery fish strayed into the Snoqualmie and Skykomish rivers, respectively, and became part of the wild population. For fish from the Wallace Hatchery, however, we assumed that 1% and 28% of adults strayed into the Snoqualmie and Skykomish rivers, respectively (Kit Rawson, Tulalip Tribes, and Curt Kraemer, Washington Department of Fish and Wildlife, 16018 Mill Creek Boulevard, Mill Creek, WA 98012, USA, unpublished data).

Harvest policies

Fish in the ocean mature at age-specific rates. If the model application is to include fishery catch, those fish maturing in the ocean and returning to freshwater are then subject to harvest. We allowed for two possible harvest management policies: a constant escapement goal or a constant harvest rate. When managing for constant escapement, the model allows a set number of adult fish to "escape" the fishery and return to freshwater before harvesting the remaining spawners. Under a constant harvest rate policy, the model treats harvest as another source of mortality by taking a set proportion of the returning adult fish (z_t). Therefore, the harvest rate for a given year (z_t) becomes

$$(11)\quad z_t = \begin{cases} 1 - \dfrac{\text{escapement}}{\sum \text{adults}} & \text{if constant escapement policy} \\ z_t & \text{if constant harvest policy} \end{cases}$$

The harvest rate on wild and hatchery fish is potentially stochastic, and if so, the realized harvest rate (z^*) becomes

$$(12)\quad z_t^* = z_t \varepsilon_t$$

where ε_t is a random variate drawn from a uniform, normal, or lognormal distribution. For our purposes, we only adopted a constant harvest rate policy with $z_t = 0.22$ with $\varepsilon_t \sim N(1.0, 0.02)$ based on data from 1999–2003 provided by the comanagers (Kit Rawson, Tulalip Tribes, and Curt Kraemer, Washington Department of Fish and Wildlife, 16018 Mill Creek Boulevard, Mill Creek, WA 98012, USA, unpublished data). Some fish from the Snohomish are caught at sea in troll fisheries, but the majority are harvested within Puget Sound in gillnet and purse-seine fisheries. We made no distinction between the two nor did we consider size-selective harvest. We also assumed no change in harvest rate when moving from the current path scenario to the test policy case.

Maturation and spawning

Each year, a proportion of adults from each stock k mature based on their stage s ($m_{s,k}$; Table 3). The number of fish returning to the river and subject to harvest is thus

$$(13)\quad N_{s,k,\mathrm{return},t} = m_{s,k} N_{s,k,\mathrm{ocean},t}$$

Those remaining in the ocean then follow eq. 1 and parameter values in Table 1 for transition to the next stage. The subsequent number surviving harvest and returning to the river is

$$(14)\quad N_{s,k,\mathrm{river},t} = (1 - z_t) N_{s,k,\mathrm{return},t}$$

Although all fish in the ocean are treated as one large pool, the model actually tracks them by their natal location. Some fish surviving harvest stray from their natal locations upon return based on a straying matrix (**Y**) that identifies the proportion of fish straying from a particular natal location i to a spawning area j. The number of fish spawning (S) in a location j is then

$$(15)\quad S_{s,k,j,t} = \sum_i Y_{i,j} N_{s,k,i,t}$$

For the hatchery fish returning to a reach, some (or all) are removed for hatchery egg take (E) to meet the hatchery's minimum egg quota (E_{quota}), so that

$$(16)\quad E_{s,k,i,t} = \min(S_{s,k,i,t}, E_{\mathrm{quota}})$$

Any remaining fish are allowed to spawn in the natural environment and become part of the wild stock:

$$(17)\quad S_{s,\mathrm{wild},i,t} = S_{s,\mathrm{hatchery},i,t} - E_{s,k,i,t}$$

In our case study, all of the adults returning to the Tulalip hatchery are harvested and their broodstock is taken from the Wallace hatchery, but some of the Wallace fish are allowed to spawn in the wild (Kit Rawson, Tulalip Tribes, and Curt Kraemer, Washington Department of Fish and Wildlife, 16018 Mill Creek Boulevard, Mill Creek, WA 98012, USA, unpublished data).

Table 3. The proportion of adult salmon in the ocean that mature and return to the river to spawn, by age and stock (Pam Goodman, Northwest Indian Fisheries Commission, 6730 Martin Way East, Olympia, WA 98516, USA, unpublished data) and the age-specific fecundity (eggs per female) (Greene and Beechie 2004).

		Stock-specific maturation rates (m)			
Stage (s)	Age	Wild	Tulalip	Wallace	Fecundity (f)
5	2	0.02	0.03	0.02	2500
6	3	0.13	0.18	0.14	4848
7	4	0.60	0.90	0.82	5710
8	5	1.0	1.0	1.0	6664

Spawners from all stocks (k) and areas (i) in a given year t are then transformed into total potential eggs ($N_{1,k,i,t}$) according to

$$(18)\quad N_{1,k,i,t} = \sum_s P_s S_{s,k,i,t} f_s$$

where P_s is the proportion of females of stage s (= 0.5 for all stages), $S_{s,k,i,t}$ is the number of spawners of a given stage s, and f_s is the stage-specific fecundity (Table 3).

Sensitivity analyses

As a first step toward identifying the type and location of potential restoration actions in the Snohomish River basin, we conducted a sensitivity analysis of the model following the basic parameterization for the "current path" described above. By systematically increasing the productivity or capacity estimates for various life stages while holding all other values constant, we estimated the change in the number of spawners throughout the entire basin. We did so for the following model parameters: adult capacity, juvenile (fry and smolt) capacity, egg-to-fry survival, and fry-to-smolt survival. For the capacity estimates, we replaced the estimates under the current path with those estimated under historical conditions. For the survival estimates, we simply increased those under the current path by 10% of their estimated value (e.g., an egg-to-fry survival of 5% became 5.5%). In addition to changing the parameter values across the entire basin at once, we also changed the parameter values in one of four select geographical regions (the estuary, mainstem reaches, lowland streams, and headwater streams) while keeping all others constant.

Results

The first metric for classifying viable salmon populations (VSP) is abundance. Under the current path parameterization, the model produced smolt and spawner abundances similar to those observed in the Snohomish River basin. Our mean egg-to-fry survival rate was 7.7% compared with the average 7.1% for stream-type Chinook based on data reviewed by Bradford (1995). Shiraz tended to overestimate the number of wild spawners (8383) compared with the average 3700 (95% confidence interval (CI): 3249–4146) estimated by the Puget Sound Technical Recovery Team from 1965 to 2002. Nevertheless, they have also witnessed an increase in wild spawners in recent years, with 10 600 wild fish returning in 2004. The number of modeled smolts (611 400) was close to that estimated from screw traps on the river (800 200) from 2001 to 2003 (Brian Kelder, Tulalip Tribes, 7515 Totem

Fig. 3. Modeled spawner–recruit relationships for the wild stocks only under the historical (open triangles), test case (shaded circles), and current path (solid squares) scenarios. Recruits are simply the number of adults returning to spawn.

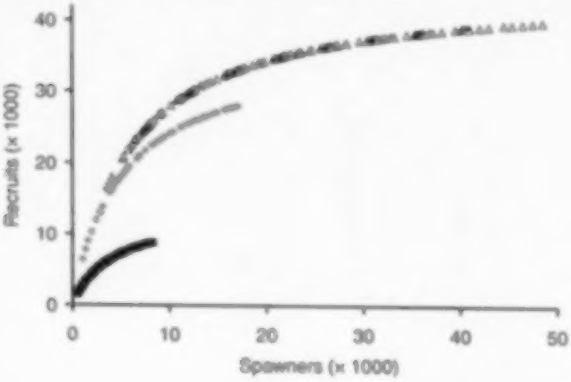
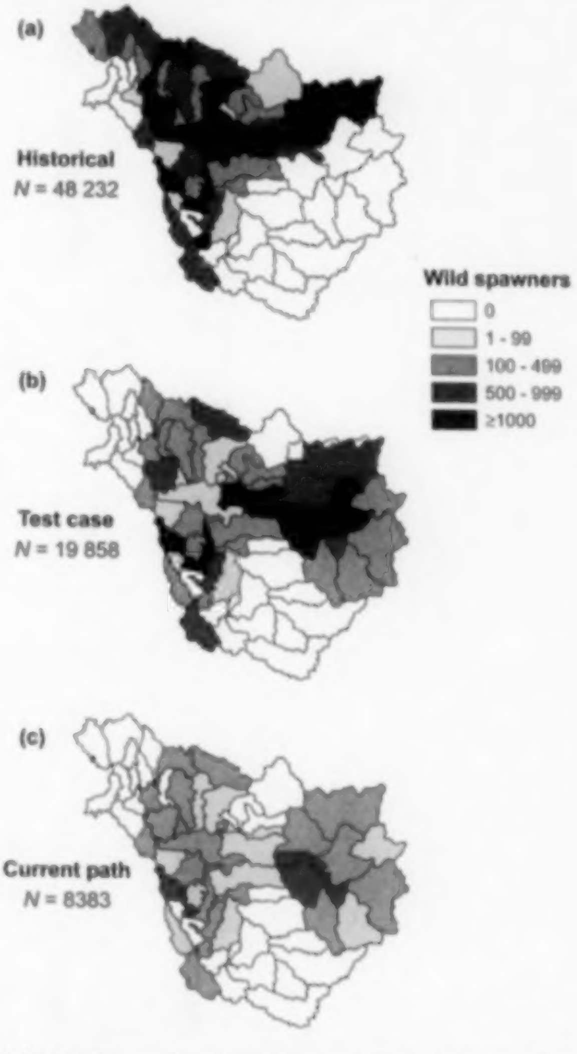


Fig. 4. Maps of the spatial distribution of the predicted number of spawners under (*a*) historical, (*b*) test case, and (*c*) current path scenarios. The estimate of the equilibrium spawner abundance is listed under each name.



Beach Road, Tulalip, WA 98271, USA, unpublished data). On average, hatchery fish constituted a majority of the returning spawners in our modeled populations, with 46% and 17% coming from the Wallace and Tulalip hatcheries, respectively. The remaining 37% of those surviving the fishery came from wild spawners or from hatchery fish that strayed and spawned in the wild. These model predictions varied somewhat from the observed stock composition where an average of 53% of spawning fish from 1971 to 2002 originated from hatcheries. From 1993 to 2002, however, hatchery fish represented 68% of the returning spawners observed in the basin, which is closer to our model result of 63%.

In addition to population abundance, stock productivity represents the second of the important VSP criteria for viable salmon populations. The estimates of productivities and carrying capacities from the stock–recruit relationship of wild fish varied under the three different scenarios (Fig. 3). For the historical case, the estimated intrinsic productivity was 7.34 recruits per spawner with a capacity of 44 881 recruits. Under current conditions, however, the estimated productivity was much lower at 3.15 recruits per spawner with a capacity of 13 203 recruits. We estimated an improvement in the test case with an estimated productivity of 7.05 recruits per spawner and a capacity of 36 359 recruits.

The abundance and spatial distribution (the third VSP criterion) of wild spawners across the landscape in the current path differed considerably from our best approximation of that under historical conditions (Fig. 4). Overall, we estimated that the Snohomish River basin currently produces only 17% of the historical number of spawners (26% if we include hatchery fish). Although only 34 of 62 subbasins currently support spawners, we estimated that 37 of them did historically. The six additional South Fork Skykomish subbasins that support spawners currently, but not historically, result from an active management decision by WDFW to truck spawners above Sunset Falls, a naturally occurring anadromous barrier. The abundance and spatial structure of spawners increased considerably under the test case (Fig. 4). We projected a 137% increase in abundance of wild fish, resulting in spawner levels that would be 41% of our historical estimate (53% of historical if we also include hatchery fish). Additionally, we found spawners expanding their range into a total of 36 subbasins, including those above Sunset Falls as we assumed that the active management would continue as currently implemented. Furthermore, the Skykomish and Snoqualmie rivers responded differently to the proposed test case such that they showed increases from the current path of 149% and 123%, respectively.

The fourth VSP attribute used to guide salmon recovery efforts throughout the Pacific Northwest is diversity, which includes genetically based variation and environmentally induced phenotypic variation in life-history traits. Although we did not model differences in genetic composition of the populations, we calculated the proportion of spawners from model runs that breed in various habitat types. We used this as an index for inferring the potential expression of varying life-history traits under different habitat, hatchery, and harvest conditions that we

Fig. 5. The proportion of spawners under historical (open bars), test case (shaded bars), and current (black bars) scenarios across a diversity of spawning habitats represented by EPA level-IV ecoregions (Omernik 1995).

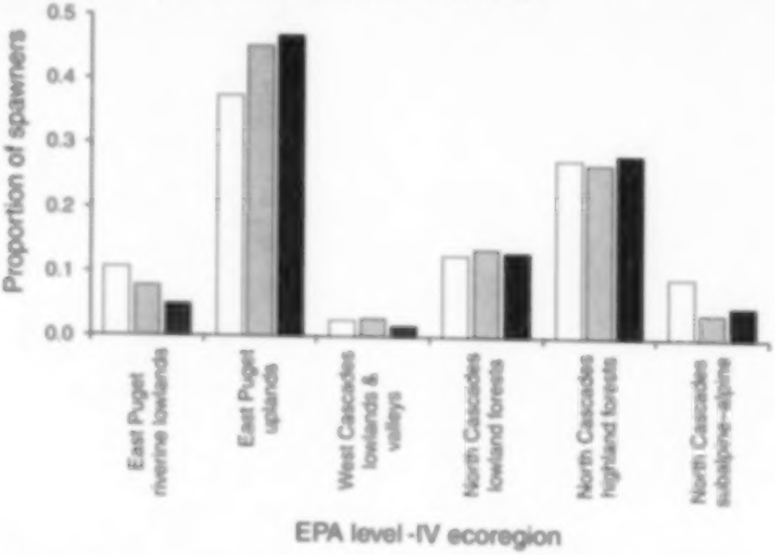
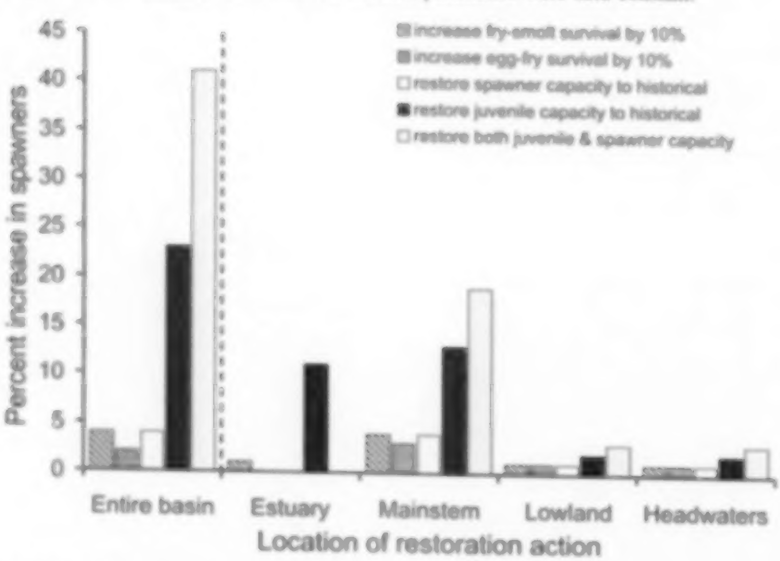


Fig. 6. Results of the initial model sensitivity analyses of the "current path" parameterization to identify appropriate restoration actions. In each case, the value of interest was increased while all other model parameters were held constant.



modeled (e.g., potential differences in spawning migration timing). By far, the majority of fish spawned in the East Puget uplands under all three scenarios, followed by North Cascades highland forests (Fig. 5). Although we found no significant differences in the percentage of fish spawning in each of the ecoregions among the three scenarios, the difference between the policy test case and historical conditions ($\chi^2 = 5.8$, df = 5, $P = 33$) was much less than that between the current path and historical condition ($\chi^2 = 7.8$, df = 5, $P = 17$).

Our sensitivity analysis revealed that increasing adult capacity had very little effect on the predicted number of spawners by itself (Fig. 6). When we increased juvenile capacity to our historical estimate, however, the predicted number of spawners increased substantially, but the effect was most prominent in the estuary and mainstem reaches, with very little impact in the peripheral lowland and headwater reaches (Fig. 6). Interestingly, we observed a synergistic effect of increasing both adult and juvenile capacity such that those improvements resulted in percentage increases in spawner abundance that were greater than the sum of the individual actions. Overall, increasing egg-to-fry or fry-to-smolt survival had less of an impact than improving capacity, but it did have a greater impact in the estuary and mainstem reaches than in the lowland and headwater reaches (Fig. 6).

Discussion

Models offer a quantitative framework for assimilating data, identifying important features of the environment, predicting future outcomes, and evaluating the potential effects of various decisions (Hilborn and Mangel 1997). In particular, life-cycle models provide scientists and policy makers with a tool for studying how changes in vital rates affect the overall population dynamics of species. In a conservation context, these models are often used to estimate population growth rates and the threat of extinction (e.g., Kareiva et al. 2000; Ellner and Fieberg 2003; Wilson 2003). In these instances, the most valuable models incorporate a variety of data related to the all of the external (e.g., habitat, exploitation) and internal (e.g., density-dependent) processes that affect the various life stages, while maintaining the flexibility to include new data or assumptions as to how the system of interest operates (Boyce 1992). The Shiraz model is designed to do just that.

Viable salmon populations (VSP) are defined by four important metrics: abundance, productivity, spatial structure, and diversity (McElhany et al. 2000). Important consideration of all of these performance measures is necessary when setting recovery goals and planning restoration actions (Boyce 1992). The Shiraz model framework allowed us to evaluate changes in these VSP parameters under various scenarios. Just as with any other model, Shiraz should be used in conjunction with empirical data and viewed as merely one of several tools available in the planning process. Scenarios offer an effective way of bringing stakeholders together to confront issues of concern (Bennett et al. 2003), and the Shiraz model framework offers the opportunity for salmon-recovery groups to explore the consequences of those scenarios for fish populations. By including harvest, hatchery, and habitat effects in the scenarios, we can obtain more realistic projections than models that consider only habitat.

By using a combination of empirical data and modeling efforts and exploring the outcomes of very different protection and restoration scenarios, we were able to present the decision makers in the Snohomish Basin Recovery Planning Group with clear choices for possible strategies. Our original sensitivity analyses suggested that restoration actions aimed at improving juvenile rearing habitat in the estuary and lower mainstem reaches would have the best chance of improving overall population performance. This essentially confirmed the independent assessment of regional biologists and planners who classified those areas as degraded (<50% intact) or moderately degraded (50%–80% intact) relative to historical conditions because of urbanization and agricultural activities (Snohomish Basin Salmonid Recovery Technical Committee 2004).

Our results indicated that the test case alternative would result in approximately 41% of the estimated historical spawner abundance. This population level would not reach the recovery goal of 80% of historical abundance adopted by the planning group (Snohomish Basin Salmonid Recovery Technical Committee 2004). Nevertheless, there are several reasons why we expect that we underestimated the potential response of salmon to recovery actions. First, our analyses do not capture the full spectrum of restoration measures proposed by the technical committee because of our inability to ascribe changes to in-stream habitat attributes from the entire suite of actions (Bartz et al. 2006). Second, the projected increases in the quantity of juvenile rearing habitat could also produce subsequent increases in the quality of available habitat and improve survival rates, a possibility that we were unable to account for in the model owing to the lack of a predictive relationship between habitat quantity and quality. Third, we used several fixed parameters from Greene and Beechie (2004) that might also improve with positive changes in habitat. For example, the survival from smolts to age-2 adults was fixed at a particularly low value (0.033), and given improvements in growth during the parr and smolt stages, we would expect concurrent increases in marine survival (Holtby et al. 1990; Koenings et al. 1993; Zabel and Williams 2002). Similar arguments would apply to our underestimates of the parameters for stock–recruit models. Fourth, improvements in spawner escapements should increase the amount of marine-derived nutrients and energy delivered to this ecosystem in the form of carcasses and gametes that are important to the growth and survival of stream-dwelling salmonids (Bilby et al. 1998; Wipfli et al. 2003) and the overall health of the surrounding ecosystem (Cederholm et al. 1999; Naiman et al. 2002; Schindler et al. 2003). Fifth, our test case used the same hatchery and harvest policies as those currently implemented in the Snohomish River basin, but future recovery decisions will almost certainly involve changes in those plans as well. Therefore, our results should be taken as a conservative estimate of the population response to the proposed restoration actions under the test case.

As mentioned above, we chose relatively few functional relationships for implementation in the Shiraz model. We did so for several reasons. First, models are only as good as their input variables, and we were limited by the availability of both habitat-specific data (e.g., temperature, fine sediment) and functional relationships for relating those data to fish productivity and capacity. Therefore, we felt it wiser to rely on literature values when we could not derive our own parameter estimates or functional relationships. Second, simpler models tend to be more generally applicable to other systems and the results are easier to understand (Gunderson and Holling 2001). Third, our goal was to develop a transparent framework for using detailed fish–habitat relationships to assess large-scale responses of fish populations to changes in habitat, hatchery operations, and harvest levels. Using relatively simple models as planning tools with a collection of stakeholders can be an important step toward effective management (Carpenter 2002; Bennett et al. 2003), and Shiraz is designed to be used in such a manner. Finally, although understanding the historical causes of population decline is important, concentrating on the potential response of fish to future remediation activities is more important for recovery efforts (Ruckelshaus et al. 2002), and the Shiraz model framework does this.

Our model structure relied on the underlying stage-specific Beverton–Holt relationship of Moussalli and Hilborn (1986). Other model forms such as the Ricker model (Ricker 1954) or a hockey stick model (Barrowman and Myers 2000) could be potentially employed, but the underlying model assumptions would need to be addressed to avoid potential problems (e.g., a nonunimodal spawner–recruit curve). We are aware of another model that also uses the multistage Beverton–Holt model to drive transitions from one life stage to another. The ecosystem diagnosis and treatment (EDT) model has also been applied to salmon restoration problems in the Pacific Northwest, but there is no formal publication describing the methods or functional relationships (see http:// www.mobrand.com/MBI/library.html). Furthermore, it does not allow for stochasticity, nor does it provide outputs of the number of individuals of a given life stage by spatial location across time.

Because the Shiraz model is a flexible framework, it could be adopted for use with other fish species, whether marine or freshwater. For example, the 1996 reauthorization of the Magnuson–Stevens Fishery Conservation and Management Act established that the conservation of essential fish habitat (EFH) is an important component of building and maintaining sustainable fisheries throughout US waters. The Act requires cooperation among the National Marine Fisheries Service, the eight regional fishery management councils, fishing participants, federal and state agencies, and others in achieving EFH protection, conservation, and enhancement. By relating the amount and kind of habitat to fish productivity and capacity, the Shiraz model easily could be used by this collection of stakeholders to establish EFH by determining the relationship of changes in both population parameters to changes to habitat.

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Appendix A

Table A1. Description of the various functional relationships between an indicator variable (X) and the response variable (Y, either p or c).

Functional relationship	Equation
Constant value	$Y = p_1$
Constant multiplier	$Y = p_1 X$
Exponential	$Y = p_1 \exp(p_2 X))$
First-order impact[a]	$Y = \exp(p_1(X - X_N))$
Second-order impact[a]	$Y = \exp(p_1(X - X_N) + p_2(X - X_N)^2)$
Third-order impact[a]	$Y = \exp(p_1(X - X_N) + p^2(X - X_N)^2 + p_3(X - X_N)^3)$
Line segments[b]	$Y = \begin{cases} f_1(X) & \text{for} \quad X \le x_1 \\ f_2(X) & \text{for} \quad x_1 < X \le x_2 \\ f_3(X) & \text{for} \quad x_2 < X \end{cases}$

[a] For first- through third-order impacts, X_N represents some normal condition against which the observed variable is compared.

[b] For line segments, $f_1(X)$ is a straight line fit between the points x_0, Y_0 and x_1, Y_1; $f_2(X)$ is a straight line fit between the points x_1, Y_1 and x_2, Y_2, etc.

Survival of Arctic cod larvae (*Boreogadus saida*) in relation to sea ice and temperature in the Northeast Water Polynya (Greenland Sea)

Louis Fortier, Pascal Sirois, Josée Michaud, and David Barber

Abstract: We tested the hypothesis that the survival of Arctic cod larvae (*Boreogadus saida*) is limited at sea ice cover >50% and sea surface temperature (SST) <0 °C. In 1993 in the Northeast Water Polynya, a spring cohort (14 May – 15 June) was hatched under heavy ice cover (58%–91%) and cold SST (–1.7 to –1.0 °C) and a summer cohort (21 June – 21 July) under low ice cover (4%–31%) and above-zero SST (1.5 to 3.9 °C). Consistent with the hypothesis, the spring cohort had almost completely vanished by age 10 days (first feeding stage), while the summer cohort survived well and dominated the population by the end of our sampling in early August. By then, the few surviving spring larvae were on average 5.7 mm longer than summer larvae (18.6 vs. 12.9 mm). A retrospective analysis of ice cover in the polynya (1979 to 2003) indicated that first-feeding larvae of the spring cohort encountered good survival conditions (sea ice <50% and SST >0 °C) in only 12% of the years compared with 80% for the summer cohort. The survival advantage provided by a larger size at the onset of Arctic winter could explain the evolutionary persistence of a spring cohort despite the low probability of initial survival.

Résumé : Nous avons testé l'hypothèse que la survie des larves de morue arctique est faible à des couverts de glace >50% et des températures de surface (SST) <0 °C. Dans les Eaux du Nord-Est en 1993, une cohorte printanière (14 mai – 15 juin) a éclos sous une banquise dense (58 % – 91 %) et à des températures basses (–1,7 à –1,0 °C), alors qu'une cohorte estivale (21 juin – 21 juillet) émergeait sous un couvert de glace léger (4 % – 31 %) et à des températures au-dessus de zéro (1,5 à 3,9 °C). En accord avec l'hypothèse, la cohorte printanière avait pratiquement disparu à l'âge de 10 jours (fin de la première alimentation), alors que la cohorte estivale a bien survécu et dominait la population à la fin de notre échantillonnage au début d'août. À ce moment, les quelques larves printanières survivantes mesuraient en moyenne 5,7 mm de plus que les larves estivales (18,6 vs. 12,9 mm). Une analyse des conditions de glace dans les Eaux du Nord-Est de 1979 à 2003 indique que les larves à la première alimentation de la cohorte printanière ont connu de bonnes conditions de survie (i.e., couvert de glace <50 % et SST >0 °C) lors de 12 % des années seulement contre 80 % pour la cohorte estivale. Une meilleure survie conférée par une plus grande taille au début de l'hiver arctique pourrait expliquer la persistance évolutive d'une cohorte de printemps malgré une faible probabilité de survie initiale.

Introduction

The warming of the lower atmosphere anticipated by general circulation models will be most intense at Arctic and sub-Arctic latitudes (e.g., Shindell et al. 1999; Flato et al. 2000). Consistent with this scenario, the maximum winter extent of the Arctic sea ice cover has shrunk by ~14% since the 1970s (Johannessen et al. 1999). The minimum summer extent of the perennial central Arctic ice pack has decreased by 9% per decade since 1979 (Comiso 2002). In September 2002 and 2005, Arctic sea ice extent and area reached successive minima since the beginning of satellite observations in 1978 (Serreze et al. 2003; NSIDC 2005). Given that global atmospheric temperatures will continue to rise over the present and next century (IPCC 2001), this decreasing trend in the extent of Arctic sea ice is not expected to reverse.

A climate-change-induced lengthening of the ice-free season in Arctic and sub-Arctic seas will severely impact species that depend on sea ice (Tynan and DeMaster 1997), potentially leading to the replacement of Arctic communities by temperate assemblages. Evidence of such impacts is accumulating. For instance, in western Hudson Bay, emaciation and reduced reproduction success of polar bears are attributed to the lengthening of the ice-free season during which the bears cannot hunt seals on the ice (Stirling et al. 1999). A shift in the diet of thick-billed murres (*Uria lomvia*) from an Arctic fish assemblage dominated by Arctic cod (*Boreogadus*

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saida) to a boreal assemblage dominated by capelin (*Mallotus villosus*) has been linked to the same lengthening of the ice-free season (Gaston et al. 2003).

The Arctic cod is a key species that channels a major fraction of the energy between plankton and vertebrates in the Arctic marine food web (e.g., Sekerak 1982; Bradstreet et al. 1986; Welch et al. 1992). The species is closely associated with sea ice during at least part of the juvenile and adult stage (e.g., Lønne and Gulliksen 1989; Gradinger and Bluhm 2004). During early life, the epipelagic larvae are particularly abundant in the ice-free and relatively warm waters of annually recurring polynyas, such as the Northeast Water Polynya (Michaud et al. 1996), hereafter referred to as the Northeast Water.

Michaud et al. (1996) showed that water temperature rather than prey density limited the feeding success of Arctic cod larvae in the Northeast Water. They suggested that Arctic cod larvae hatched at sub-zero temperatures in the Northeast Water in 1993 did not survive to contribute to the year class. In the present study, the age (in days) and hatch date of the larvae sampled by Michaud et al. (1996) were determined by otolith analysis. To identify windows of survival during the reproductive season, the hatch date frequency distribution of the population was compared for different age intervals (Fortier and Quiñonez-Velazquez 1998; Sirois and Dodson 2000). In particular, we tested the hypothesis that early survival of Arctic cod larvae is restricted to periods of low ice concentration and above-zero sea surface temperature (SST).

Materials and methods

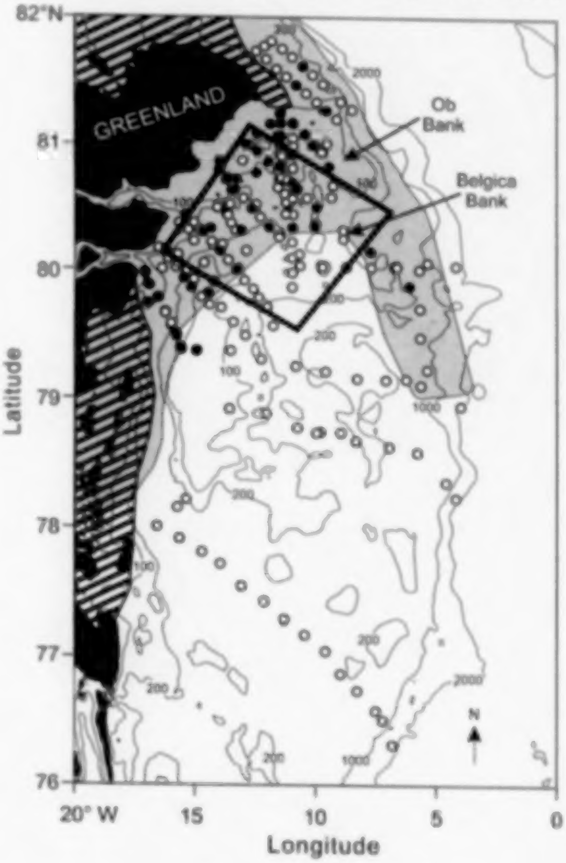
Study area

The Northeast Water is the largest and northernmost polynya along the east coast of Greenland (Fig. 1). It is bounded by the Arctic Ocean to the north and by the Polar Front of the Greenland Sea to the east and south (Smith et al. 1990). When fully opened, the polynya extends over Ob and Belgica banks on the East Greenland Shelf (Fig. 1). Water depth varies from 100 m on the banks to over 500 m in the trough system around Belgica Bank. The Northeast Water usually opens in April or May, reaches its maximum extent of ~44 000 km^2 in July–August, and closes around September (Wadhams 1981; Smith et al. 1990). A cold, low-salinity surface layer of polar origin (about 100 m thick) lies over saltier and warmer Arctic intermediate water (Schneider and Budéus 1994). The surface layer is characterized by an anticyclonic circulation around Belgica Bank (Bourque et al. 1987) that tends to retain Arctic cod larvae in the Northeast Water (Michaud et al. 1996).

Percent ice cover

Daily, cloud-independent satellite images of Arctic sea ice distribution have been available from the Special Sensor Microwave Imager (SSM/I) since 1979. The pixel resolution of the SSM/I images is 25 km × 25 km. Percent ice cover in the pixel is estimated with a precision of ±5% based on a bootstrap algorithm. To relate larval Arctic cod dynamics to local sea ice concentration, percent sea ice cover in the pixel containing each of the stations sampled for zooplankton in 1993 was extracted from the SSM/I archive (Michaud et al. 1996).

Fig. 1. Map of the Northeast Water region. The shaded area represents the extent of the polynya (ice-free or partially ice-free water) in July 1993. Hatched areas indicate the ice shelves that bounded the Northeast Water to the north and south along the coast of Greenland in 1993. Symbols represents the sampling stations where Arctic cod (*Boreogadus saida*) larvae were captured (closed symbols) or not (open symbols) (Michaud et al. 1996). Isobaths are in metres. The box delineates the area over which weekly percent ice cover was extracted from Special Sensor Microwave Imager (SSM/I) archives over the period 1978–2003.



To describe interannual variability in the opening of the Northeast Water, percent ice cover in the general area of the opening of the Northeast Water (Fig. 1) was averaged for each week in the period 1979–2003. For a given year, we defined the opening of the Northeast Water as the week in summer when ice cover first reached 50% or less and the closing of the polynya as the week when ice cover increased again over 50%.

Sampling of fish larvae

Arctic cod larvae were collected during the two legs of the expedition of the German research icebreaker RV *Polarstern* in the Northeast Water from 23 May to 20 June and 28 June to 2 August 1993. Details of sampling methodology are given in Michaud et al. (1996). In summary, young fish were collected with two different gears. At 240 stations, a 60 cm Bongo net (200 and 500 μm mesh) was hauled vertically from 200 m (or the bottom at stations shallower than 200 m) to the surface. A vertical profile of temperature and salinity was recorded at each Bongo station by a conductivity–temperature–depth (CTD) profiler. At 55 of the Bongo stations, a rectangular midwater trawl (RMT) was deployed in a double oblique tow (or triple oblique at shallow stations) down to 60 m at a towing speed of 2 knots. The RMT was equipped with two nets of 1 and 8 m^2 aperture and 300 and 2000 μm mesh, respectively; a TSK flowmeter; and a self-contained CTD to record depth, temperature, and salinity. In total, 861 larvae in the range 6–24 mm were collected, most of them (774) by the RMT. The vertical Bongo tows captured small (<8.5 mm) larvae only, while the RMT captured larvae of all sizes. SST for all stations was extracted from the CTD records.

Length and age determination

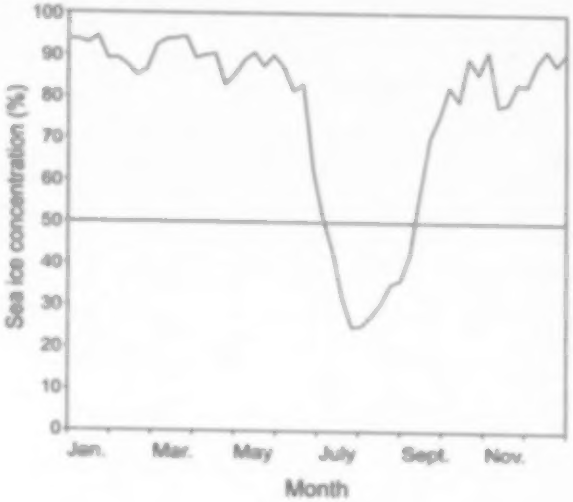
At sea, all young fish were sorted from the zooplankton collections and preserved in 95% ethanol. In the laboratory, the notochord length of 823 intact specimens was measured under the dissecting microscope. The right or left lapilli of 448 larvae were mounted in Permount on glass slides and analysed under a microscope linked to an image analyser. The lapilli of Arctic cod larvae are circular with a well-defined core and hatch mark. Recently, our team has confirmed that increments are formed daily, using tetracycline and alizarine to mark the otoliths of Arctic cod larvae collected in the North Water Polynya (northern Baffin Bay) and reared on the ship at the near-zero temperatures prevailing at capture (P. Sirois and L. Fortier, unpublished data). In the present study, a first operator enumerated the increments on 308 lapilli and a second operator on 233 lapilli, with 93 otoliths interpreted by both operators. The increment counts differed on average by 1.00 (standard deviation (SD) = 0.88 increment) between the two operators, and the slope of the regression between the two estimates (slope = 1.0011, r^2 = 0.989, n = 93) did not differ significantly from 1 (t test, P > 0.9). The counts of the first operator were retained for these 93 otoliths.

Length–age keys were used to estimate the age of the 374 larvae not aged by otolith analysis (Kimura 1977). Larvae in a given 1 mm length class were randomly attributed an age according to the age probability function for that 1 mm length class. Hatch date was estimated by subtracting age from date of capture.

Hatch date frequency distributions (HFDs)

Arctic cod larvae hatched within the same interval of three calendar days (starting on 8 May) were grouped into 3-day subcohorts. The number of larvae in each subcohort was used to build the uncorrected HFD for the age intervals 0–5, 6–10, 11–20, 21–40, and 41+ days at capture. Sampling discontinuities, such as the 8-day interval between the two legs of the expedition, created gaps in the HFDs (Fortier and Quiñonez-Velazquez 1998). As well, the end of sampling truncated the right-hand tail of the HFDs, the more severely so for older age intervals. This is because larvae hatched on a given day cannot be present in the HFD of a given age interval if sampling has stopped before the larvae reached this age interval. The periods during which Arctic cod larvae in different age intervals (i.e., 0–5, 6–10 days, etc.) were not vulnerable to sampling are presented with the HFDs.

Fig. 2. Annual cycle of sea ice concentration (% cover) in the Northeast Water in 1993. Weekly percent ice cover was extracted from the Special Sensor Microwave Imager (SSM/I) archives over the area given in Fig. 1.



For a given age interval, a subcohort comprising young larvae will be over-represented in the HFD relative to a subcohort comprising older larvae that have experienced mortality and dispersion for a longer period (Campana and Jones 1992). The rate of loss by mortality and dispersion out of the sampling area was estimated by adjusting an exponential decay model to the descending limb of the catch curve for each cohort. This approach assumes a constant exponential rate of mortality–dispersion and that no new larvae recruit to the population after the initial hatching. The HFDs were corrected by subtracting from each subcohort the number of larvae that would have been lost during the interval between the average age of that subcohort and the upper boundary of the age interval considered (Yoklavich and Bailey 1990; Fortier and Quiñonez-Velazquez 1998). For example, if the average age at capture of larvae in a given subcohort of the HFD for the 11–20 day age interval was 15 days, the number of larvae in that subcohort was reduced in proportion to the percent loss that would have been suffered over the interval from age 15 to age 20 days, based on the mortality–dispersion curve.

Results

Ice cover concentration in 1993

In 1993, percent ice cover in the general area of the Northeast Water oscillated between 82% and 95% over the period from January to mid-June and then decreased rapidly to 25% by the third week of July (Fig. 2). Percent ice cover increased slowly during August and then faster in September. Ice cover extended back to 80%–90% by the end of September.

Fig. 3. The regression of age (days) on notochord length (mm) in larval Arctic cod (*Boreogadus saida*) sampled in the Northeast Water in 1993 and aged through otolith analysis. The age probability function for a given 1 mm length class was used to assign an age to larvae that were not aged by otolith analysis. (age = 4.295 length − 29.9; r^2 = 0.966).

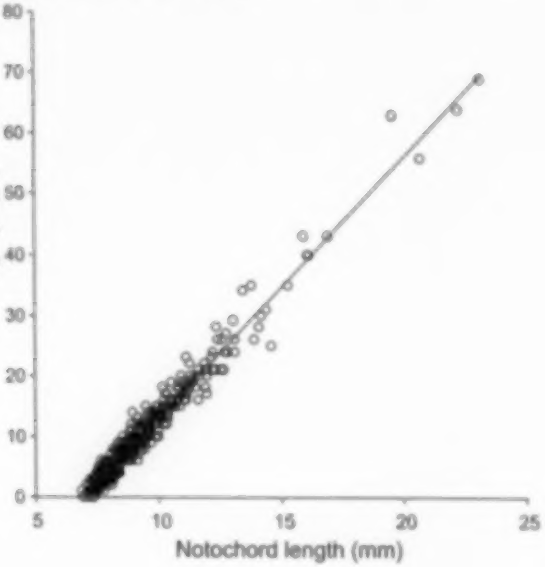
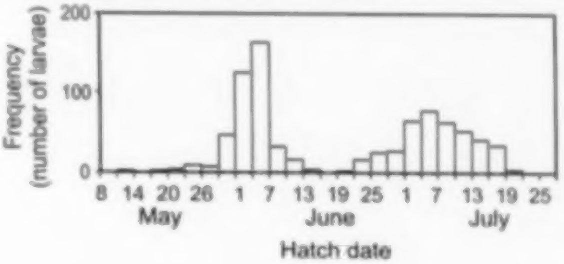


Fig. 4. Hatch date frequency distribution (HFD) for all larvae (n = 823) of Arctic cod larvae (*Boreogadus saida*) sampled in the Northeast Water region from 23 May to 2 August 1993. The HFD is not corrected for mortality and dispersion. Larvae hatched in the same 3-day calendar interval were grouped into a subcohort represented by a single histogram.



In 1993, the polynya opened (<50% ice cover) in the first week of July and closed (>50% ice cover) in the second week of September.

Uncorrected hatch date frequency distributions of Arctic cod larvae

Age was strongly and linearly correlated to notochord length for the 448 larvae aged by otolith analysis (Fig. 3), enabling us to use age–length keys to estimate the age of the remaining 374 intact larvae from their notochord length.

Two distinct cohorts were evident in the overall HFD for all the Arctic cod larvae sampled in 1993 (Fig. 4). A spring cohort was hatched from as early as 11 May to 16 June, but with few larvae emerging before 21 May. A distinct summer cohort was hatched from 21 June to 21 July (Fig. 4). The respective modes of the HFDs of the spring (4–7 June) and summer (4–7 July) cohorts were separated by 1 month (Fig. 4).

The HFDs (uncorrected for mortality–dispersion) were compared among different intervals of age at capture (Fig. 5). Gaps in the HFDs corresponded precisely to periods of nonvulnerability to our sampling. Finding larvae of a given age interval hatched inside these periods would have indicated ageing errors. The fact that none of the 823 estimated hatch dates fell inside these periods of nonvulnerability supports the accuracy of the age estimates.

The spring cohort comprised 88.6% of the total number of larvae in the 0–5 day age interval and was hatched from 21 May to 17 June (Fig. 5*a*). This initially abundant spring cohort represented only 14.2% of the larvae in the 6–10 day age interval (Fig. 5*b*). It was absent from the 11–20 day age interval (Fig. 5*c*) and was represented by three individuals only in the 21–40 day age interval (Fig. 5*d*). The seven larvae older than 41 days sampled in 1993 (16–23 mm in length and 43–69 days old) belonged to this spring cohort (Fig. 5*e*).

Newly hatched larvae of the summer cohort represented 11.4% of the larvae in the 0–5 day age interval collected in 1993 (Fig. 5*a*). Our sampling likely missed the 0- to 5-day-old larvae hatched from 22 June to 4 July, which were detected in the 6–10 and 11–20 day age intervals (Figs. 5*a*–5*c*). Contrary to the spring cohort, the summer cohort persisted in the 11–20 and 21–40 day age intervals (Figs. 5*b*–5*d*). The right-hand tail of the HFDs was progressively truncated as the period of nonvulnerability to sampling extended back in time for progressively older larvae. Likewise, larvae of the summer cohort older than 41 days could not be sampled, as the ship had left the study area before they reached that age (Fig. 5*e*).

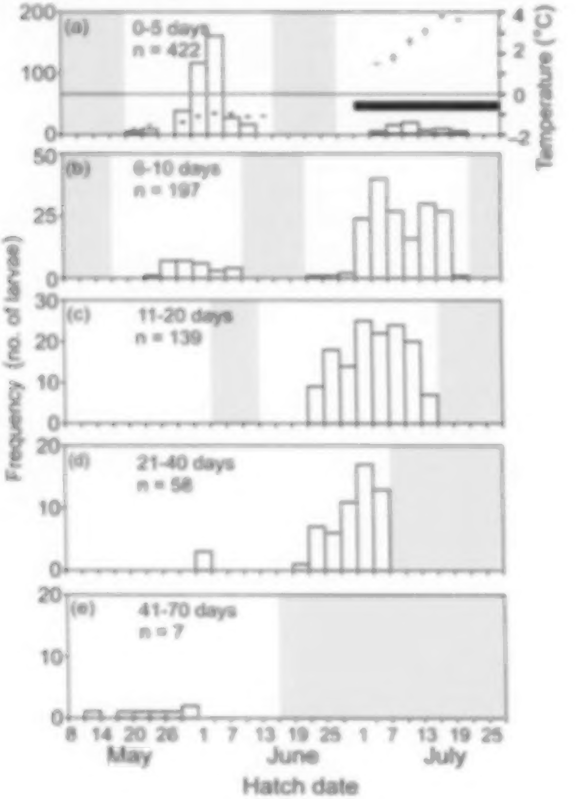
The SST and the percent ice cover prevailing at capture was averaged for each 3-day subcohort of 0- to 5-day-old larvae. Newly hatched subcohorts of the fast-disappearing spring cohort experienced SST ranging from −1.7 to −1 °C (Fig. 5*a*) and ice cover ranging from 58% to 91%. Subcohorts of the persisting summer cohort were hatched at SST temperatures ranging from 1.5 to 3.9 °C (Fig. 5*a*) and ice cover ranging from 4% to 31%.

Hatch date frequency distributions corrected for mortality–dispersion

The number of Arctic cod larvae collected decreased exponentially with age (Fig. 6). For the spring cohort, losses by mortality and potential dispersion outside the sampling area were remarkably high and averaged 63.3% per day over the first 10 days of life (Fig. 6*a*). The rate of decay of the summer cohort was calculated for the descending limb of the catch curve (Fig. 6*b*). At 13.9% per day, the mortality–dispersion of the summer cohort was much slower than that of the spring cohort.

The uncorrected HFDs compare the abundance of subcohorts of different average age that have suffered mortality and dispersion for different times. For example, in the HFD for the 0–5 day age interval, the average age of Arctic cod larvae in the eight subcohorts forming the spring cohort ranged from 1 to 5 days. The bias in the HFDs due to differences in age among the subcohorts was removed by reducing

Fig. 5. Hatch date frequency distributions (HFDs) of larval Arctic cod (*Boreogadus saida*) sampled in the Northeast Water region from 23 May to 2 August 1993 by age intervals. The HFDs are not corrected for mortality and dispersion. Shaded areas represent periods of nonvulnerability of the larvae to our sampling for a given age interval. The average sea surface temperature (with standard deviation) prevailing over the first 5 days of life of each subcohort is indicated in panel *a*. The thick horizontal line in panel *a* illustrates the period of opening of the polynya (<50% ice cover) that extended from the first week of July to the second week of September in 1993.

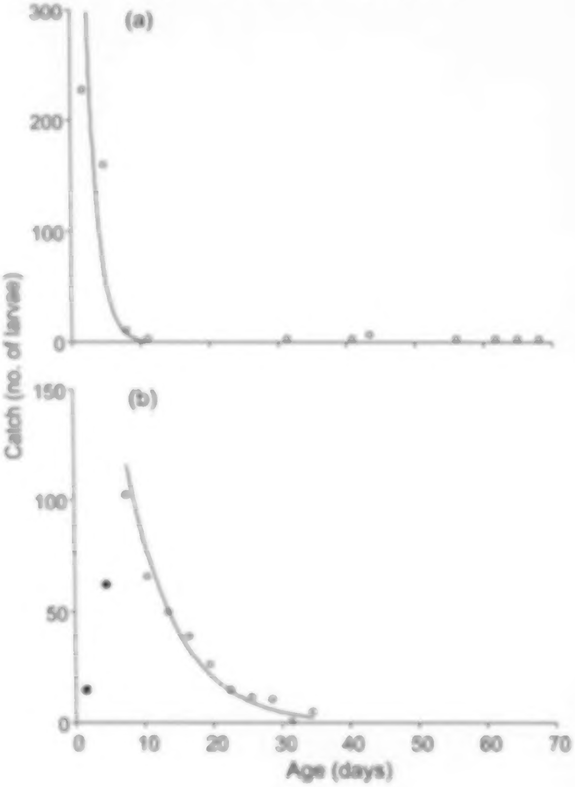


the abundance of each subcohort in proportion to the mortality–dispersion that would have been suffered over the time needed to reach the upper limit of the age interval considered (Fig. 7). The mortality–dispersion rate calculated for each cohort was applied to the respective spring and summer subcohorts. This standardization of subcohort abundance to a constant age (the upper limit of the age interval considered) results in a more accurate representation of the HFDs. The two cohorts, their relative importance, and their persistence over time changed relatively little after the HFDs were corrected for mortality–dispersion (compare Figs. 5 and 7). The main effect of the correction was to emphasize the quick disappearance of the spring cohort over the 6–10 day age interval (Fig. 7).

Advection of Arctic cod larval cohorts

Spatially, the distribution of the larvae of the spring and summer cohorts differed little at different ages (Fig. 8). For the spring cohort, the respective distributions of 0- to 5- and 6- to 10-day-old larvae coincided in the western sector of the polynya, along the Greenland Coast (Fig. 8*a*). Five of the seven larvae >41 days old (43–69 days old) were captured in the same general area; two larvae were captured further east (Fig. 8*a*). A similar pattern was observed for the summer cohort, with all age intervals generally concentrated in the western sector of the Northeast Water except for a few older larvae of the 11–20 and 21–35 day age intervals captured eastward (Fig. 8*b*).

Fig. 6. The regression of catch at age for the (*a*) spring (catch = 1125 $e^{-0.613age}$; $r^2 = 0.929$) and (*b*) summer (catch = 333 $e^{-0.139age}$; $r^2 = 0.833$) cohorts of larval Arctic cod (*Boreogadus saida*) sampled in the Northeast Water in 1993 and grouped in 3-day age subcohorts. In panel *b*, the exponential decay model was fitted to the descending limb of the curve with the two points represented by closed symbols excluded from the regression. The slope of the model was used as an estimate of the rate of loss of larvae due to mortality and dispersion out of the sampling area.

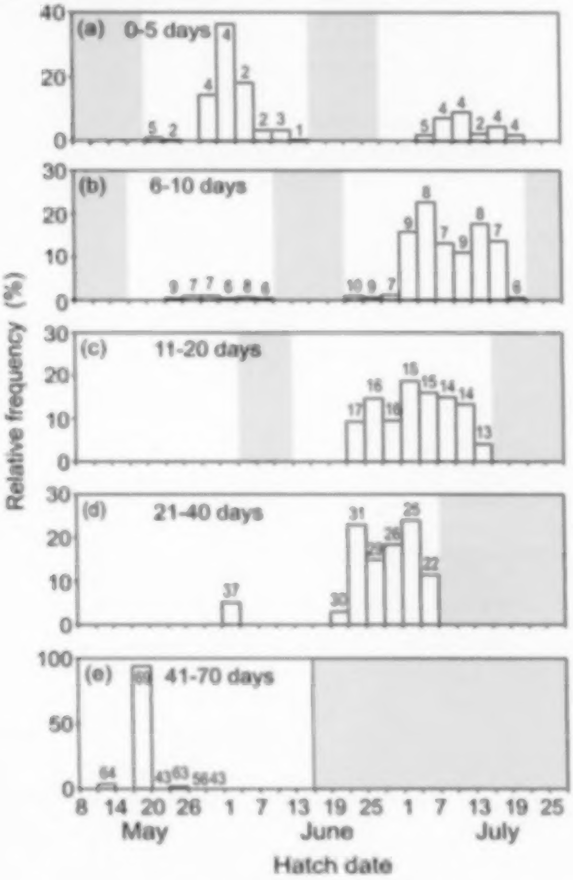


Interannual variability in the opening of the Northeast Water

The season of opening of the Northeast Water (<50% ice cover) varies considerably in timing and duration from year to year (Fig. 9). The polynya opened for less than 2 weeks in 1999, for 1 month or less in 1980 and 1994, and for nearly 4 months in 1990 and 1991 (Fig. 9). It opened as early as 1 June in 1995 and as late as 15 August in 1994.

Assuming that a spring cohort and a summer cohort of Arctic cod larvae are hatched every year over the same periods

Fig. 7. Hatch date frequency distributions (HFDs) of Arctic cod larvae (*Boreogadus saida*) by age intervals after correction for mortality and dispersion. The number above each histogram is the average age (in days, rounded to unity) of the larvae in the subcohort. Periods of nonvulnerability to our sampling are indicated by shaded areas.



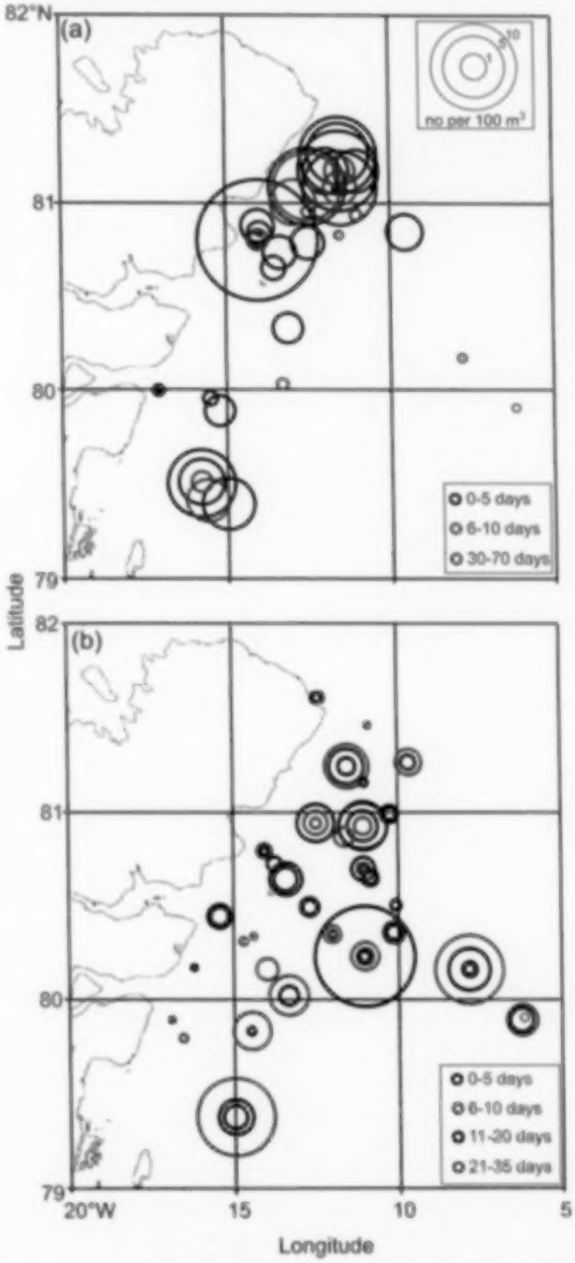
as observed in 1993, the spring cohort would have developed in open waters (<50% ice cover) and at SST > 0 °C in 3 out of the 25 years (12%) from 1979 to 2003 (Fig. 9). The summer cohort would have experienced open waters and SST > 0 °C in 20 out of 25 years (80%).

Discussion

The fate of Arctic cod larval cohorts in the Northeast Water in 1993

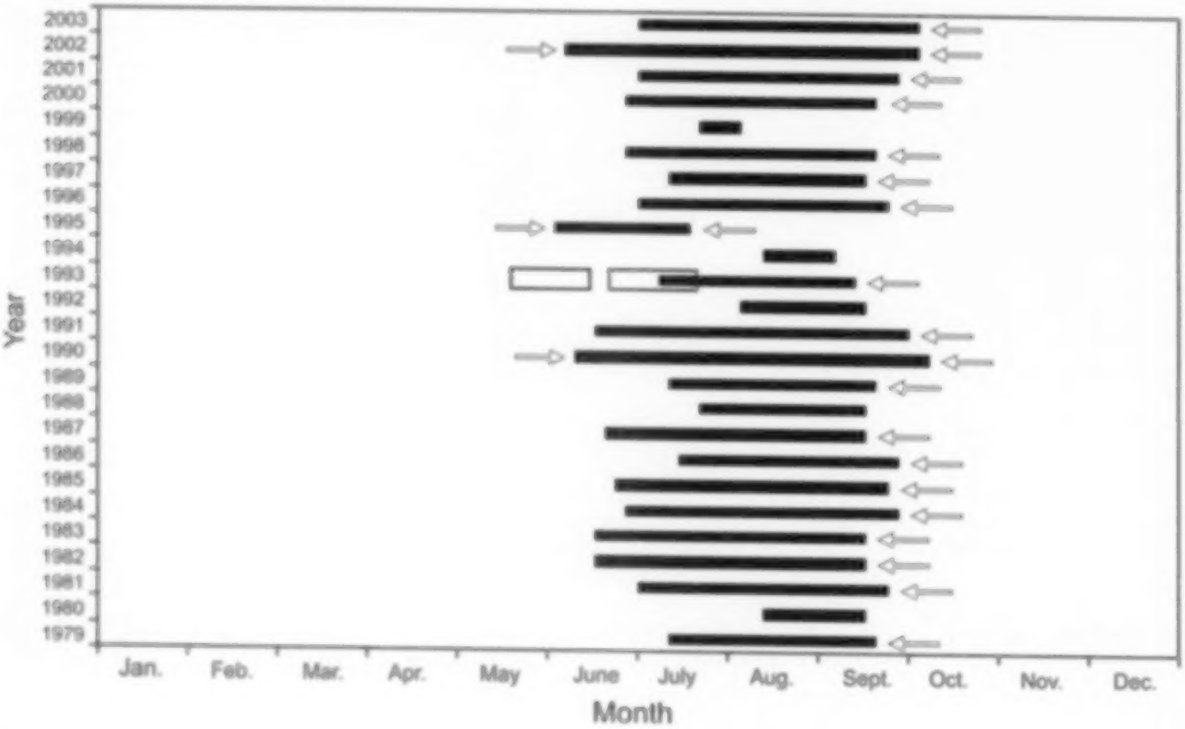
Ideally, sampling at sea to establish HFDs should be continuous and should cover the entire hatching season, so that the probability of a larva to be represented in the HFDs is independent of its hatch date (Campana and Jones 1992; Fortier and Quiñonez-Velazquez 1998). Sampling should also extend well beyond the season of hatching to document the fate of late cohorts. Continuous sampling over several months is logistically difficult, particularly in Polar seas. In the present study, except for a 9-day interruption in late June, sampling in the Northeast Water covered the hatching season of Arctic cod relatively well. But the termination of sampling on 2 August prevented monitoring the fate of the larvae hatched late in summer.

Fig. 8. Changes in the spatial distribution of larvae of different age intervals for the spring (*a*) and summer (*b*) cohorts of Arctic cod (*Boreogadus saida*) sampled in the Northeast Water in 1993. The abundance of the larvae (number per 100 metres cubed) is proportional to the area of the circle. Zero abundance values are not plotted. Age intervals are color-coded.



The seasonal pattern of production of Arctic cod larvae has been documented primarily from the seasonal occur-

Fig. 9. Seasonal opening of the Northeast Water from 1979 to 2003. Horizontal bars indicate the period during which sea ice cover was <50% in the main area of opening of the Northeast Water. The open rectangles in 1993 correspond to the production of the spring and summer cohorts of Arctic cod larvae (*Boreogadus saida*). Right-pointing arrows indicate years in which the spring cohort would have overlapped to some extent with the open (<50% ice cover) waters. Left-pointing arrows indicate years in which the summer cohort would have overlapped with open waters.



rence of the recently hatched larvae. In the Barents Sea, newly hatched larvae occur in March–April and then massively in May and June (Baranenkova et al. 1966), suggesting the production of two distinct cohorts at an interval of about 1 month. As well, the length–frequency distributions at date of Arctic cod larvae sampled in Lancaster Sound (Canadian Archipelago) in the summer of 1976 presented two modes separated by ~6–8 mm (Sekerak 1982, his fig. 7) or 26–34 days based on our age–length relationship (this study). In sub-Arctic coastal Hudson Bay, where a recurrent coastal polynya prevails in spring (Smith and Rigby 1981), Drolet et al. (1991) and Ponton et al. (1993) documented the emergence under the ice of a cohort of Arctic cod larvae in spring (mid-April to mid-May), but an eventual summer cohort was not detected by their limited sampling in July and August (Ponton et al. 1993). In the present study, the HFDs confirmed the production of distinct spring and summer cohorts of larvae at an interval of 1 month, as reported by Baranenkova (1966) and Sekerak (1982). While the presence of small, hatch-size larvae from late May to early July indicated a protracted hatching period, these two cohorts could not be differentiated unambiguously based on the length–frequency distributions at date in the study of Michaud et al. (1996). We suspect that future otolith-based studies may confirm the prevalence of the production of two distinct larval cohorts of Arctic cod in other regions of the Arctic Ocean.

While the spring cohort almost completely disappeared from our collections in the Northeast Water area early in the larval stage, the 10 late larvae (31–69 days of age) belonging to this cohort captured in July–August confirmed that some individuals hatched in spring survived life in the plankton. However, survival until 40 days of age was much superior for the initially less abundant summer cohort than for the spring cohort. Again, the absence of larvae ≥41 days old in the summer cohort is an artefact due to the ship leaving the area before the fish had reached that age. Indications are that this cohort would have dominated the HFDs of larvae ≥41 days of age if sampling had been pursued over August and September. Extrapolating from the HFDs, we conclude that the summer cohort likely made up the bulk of the population of pelagic juveniles that survived the planktonic larval stage to overwinter in 1993.

There are two potential explanations for the quick reduction in the abundance of the spring cohort of Arctic cod larvae in the Northeast Water in 1993. First, the larvae hatched in spring could have been dispersed out of the sampling area before they reached 11 days of age (or ~9.5 mm in length). However, the spatial distribution of the spring cohort differed little for different ages, indicating little net transport in any direction save for the tendency for some of the older larvae (30–70 days of age) to occur southeast of the general distribution of the population. This limited southeast transport of the larvae is consistent with the anticyclonic surface circulation reported for the Northeast Water (Bourque et al. 1987). Hence, we found no indication that the quick loss of the spring cohort was linked to their rapid advection out of the sampling area. Our analysis suggests a very slow anticyclonic advection of the two cohorts along the slope of Belgica Bank. Such an anticyclonic retention pattern has often been reported for the larvae of fish spawning over shelf banks (see Heath 1992 for a review).

The second explanation is that few larvae of the spring cohort actually survived the transition from endogenous nutrition to exogenous feeding that follows the exhaustion of yolk reserves. Yolk sac resorption in Arctic cod larvae occurs at a length of ~8.5 mm (Michaud et al. 1996), corresponding to an age of ~6 days. Hence, the disappearance of the spring cohort from our collections by the time the larvae reached 11 days of age coincided, on average, with the end of the first 5 days of exogenous feeding. This observation is consistent with the long-standing hypothesis that failure to successfully initiate exogenous feeding at the time of yolk resorption results in mass mortality (Hjort 1914; Platt et al. 2003).

A majority of hypotheses on recruitment variability in marine fishes invoke prey density or the contact rate with prey as the proximate factors limiting feeding success, growth, and survival in the plankton (see review by Cowan and Shaw 2002). In the Northeast Water in 1993, the feeding success of Arctic cod larvae was not limited by the density of its main prey, copepod nauplii, but increased linearly with SST (Michaud et al. 1996). Our observations confirm that in the frigid waters of Arctic seas, temperature <0 °C during the days after the onset of exogenous feeding lead to poor survival. As reported for other oceanographic discontinuities where prey concentrations are often superabundant (e.g., fronts, river plumes, gyres), physical factors rather than trophic interactions seem to control early fish survival in polynyas.

Climate and the early survival of Arctic cod

The observation of two separate cohorts of newly hatched larvae suggests that Arctic cod in the Northeast Water has developed two distinct reproduction strategies. Early spawners produce a spring cohort of larvae with a low probability (12%) of hatching in the <50% sea ice cover and >0 °C surface waters necessary for optimum first feeding and high survival. Late spawners produce a summer cohort with a high probability (80%) of encountering these favourable conditions. Despite the low probability of encountering favourable survival conditions, the obvious adaptive value of early spawning is that the spring cohort benefits from a substantially longer (by 1 month) prewinter growth season than the summer cohort. In late July 1993 in the Northeast Water, survivors of the spring cohort were on average 18.6 mm long (±3.0 mm SD, *n* = 10), while those from the summer cohort were 12.9 mm long (±0.9 mm SD, *n* = 55). Maximizing prewinter development, size, and body reserves is a strategy common to many Arctic zooplankton species (e.g., Conover and Huntley 1991). A large size and the associated superior predatory and predator-avoidance competences likely provide Arctic cod larvae of the spring cohort with a higher probability of surviving the winter months than their summer counterparts. The survival advantage provided by a larger size at the onset of the Arctic winter could explain the evolutionary persistence of a spring cohort despite the low probability of initial survival. The growth advantage provided by early hatching could be particularly important in those infrequent years when the polynya opens unusually early. In such years, a large fraction of the spring cohort could be expected to survive life in the plankton, achieve a large prewinter size, and survive the first winter.

The winter spawning of Arctic cod is seen as an evolutionary adaptation to match the hatching of the larvae with enhanced secondary production at the marginal ice zone in spring (e.g., Ponomarenko 1967; Graham and Hop 1995). Our observations in the Northeast Water lead to the hypothesis that populations reproducing in recurring polynyas have further adapted their spawning strategies to exploit the (potential) early regression of the sea ice cover by producing a spring cohort in addition to a summer cohort of larvae. In a context of Arctic climate warming (ACIA 2005), early ice cover melt and above-zero SST would favour the growth and survival of the spring cohort and, presumably, the overwinter survival of the juveniles issued from this cohort. Therefore, at least in the short term, the lengthening of the ice-free season presently observed in Arctic seas (e.g., Comiso 2002; Serreze et al. 2003; NSIDC 2005) could result in improved recruitment and larger populations of Arctic cod. However, Arctic cod is a specialist adapted to sub-zero temperatures (e.g., Enevoldsen et al. 2003) and life close to and even inside sea ice (see Gradinger and Bluhm 2004 for a recent review). Hence, in the longer term, the progressive warming of Arctic seas and the reduction of the sea ice habitat could spell the replacement of this key species of the Arctic marine food web by less specialized sub-Arctic or temperate fishes (Tynan and DeMaster 1997; Gaston et al. 2003; Perry et al. 2005).

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Impact-recovery patterns of water quality in temporary wetlands after fire retardant pollution

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Abstract: Fire retardants, which are used in wildland fire prevention and extinguishing operations, can cause eutrophication of surface waters. We measured water quality in artificially constructed outdoor ponds over three hydrological cycles to determine impact-recovery trajectories in retardant-contaminated, temporary wetlands. We used a multiple before–after control–impact (MBACI) design to determine the effects of application rates that are used in grasslands ($1\ \mathrm{L{\cdot}m^{-2}}$) and scrublands ($3\ \mathrm{L{\cdot}m^{-2}}$). Retardant application caused a significant increase in the trophic status of the ponds in the postcontamination period (second and third hydrological cycle) relative to the precontamination period (first hydrological cycle). The retardant clearly affected nutrients and indirectly affected chlorophyll *a*, pH, dissolved oxygen, and Secchi transparency, resulting in a shift from clear water to turbid water stable states. Univariate analyses showed that water quality variables showed distinct recovery trajectories, as influenced by natural, seasonal changes (chiefly water level fluctuations). Nonmetric, multidimensional scaling analyses suggest that water quality did not return to precontamination levels after two hydrological cycles in the retardant-treated ponds. Water quality affected by retardant contamination appeared to maintain wetlands in hysteresis for at least two hydrological cycles and prevented them from returning to the clear water, submerged macrophyte-dominated state.

Résumé : Les retardants de flamme , utilisés dans la prévention et l'extinction des incendies dans les terres sauvages, peuvent causer une eutrophisation des eaux superficielles. Afin de déterminer les trajectoires impact-récupération dans des terres humides intermittentes contaminées par les retardants, nous avons mesuré la qualité de l'eau dans des étangs artificiels extérieurs pendant trois cycles hydrologiques. Nous utilisons un plan d'expérience multiple de type avant–après témoin–impact (MBACI) pour déterminer les effets des taux d'application utilisés dans les steppes ($1\ \mathrm{L{\cdot}m^{-2}}$) et les brousses ($3\ \mathrm{L{\cdot}m^{-2}}$). L'application de retardants augmente significativement le statut trophique des étangs dans la période qui suit la contamination (deuxième et troisième cycles hydrologiques) par comparaison à la période précédant la contamination (premier cycle hydrologique). Le retardant affecte nettement les nutriments et influence indirectement la chlorophylle *a*, le pH, l'oxygène dissous et la transparence de Secchi, ce qui se traduit par un passage d'un état stable d'eau claire à un d'eau turbide. Des analyses unidimensionnelles montrent que les variables de la qualité de l'eau suivent des trajectoires de récupération distinctes sous l'influence des changements naturels et saisonniers (principalement des fluctuations du niveau de l'eau). Des analyses de cadrage multidimensionnel non métrique indiquent que la qualité de l'eau dans les étangs traités aux retardants ne revient pas aux niveaux antérieurs à la contamination après deux cycles hydrologiques. La qualité de l'eau affectée par la contamination par les retardants semble maintenir les terres humides en hystérèse pendant au moins deux cycles hydrologiques et les empêche de revenir à leur état d'eau claire et de domination par les macrophytes submergés.

[Traduit par la Rédaction]

Introduction

Temporary wetlands are unique, aquatic, island-like ecosystems that are embedded in a matrix of terrestrial ecosystems. They contribute substantially to local and regional biodiversity and provide a series of ecosystem services (Gibbs 1993, 2000; Colburn 2004). Yet, temporary wetlands are less well studied in comparison with lake and river ecosystems, and land use change, contamination, and other forms of anthropogenic stress increasingly threaten them.

Several recent studies have shown that the ecological integrity of temporary wetlands can depend a great deal on their interconnectedness, in which overland dispersal of organisms and the structure of the surrounding terrestrial matrix can be important (Hall et al. 2004). Metacommunity and metapopulation dynamics have been suggested to play an important role in ecosystem recovery after contamination events; however, the speed of recovery depends on the degree of interconnectedness, which in turn depends on gradients of biogeographical isolation (Angeler and Alvarez-

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Cobelas 2005). In addition to these regional landscape characteristics, the local insular characteristics of each wetland can be important for regulating community dynamics (Rosenzweig 1995; Brose 2001). For example, water quality has been shown to cue the emergence of plants and invertebrates banked in wetland soils (Angeler and García 2005). The loss of water quality as a result of anthropogenic stress disrupted the emergence process and led to depauperate communities.

Water quality is also known to play an important role in regulating primary production pathways in shallow aquatic ecosystems, which are characterized by mixed populations of phytoplankton and submerged aquatic vegetation (SAV). Some shallow lakes appear to be dominated by SAV, while others appear to be dominated by dense phytoplankton, a finding that has been labeled alternative stable states (Scheffer et al. 1993; Jeppesen et al. 1997). Nutrient loading, predatory fish and invertebrates, and some combinations of internal and external factors have been shown to regulate these alternative states in many temperate, European shallow lakes (Jeppesen et al. 1998). Recent research suggests that wetland ecosystems may also occur in alternative stable states and that cultural eutrophication can be important in causing the shift from the "healthy" SAV state to the degraded phytoplankton state (Chow-Fraser 1998; Alvarez-Cobelas et al. 2001).

A form of anthropogenic stress that may affect the ecosystem processes and ecological integrity of wetlands as depicted above is the contamination with fire retardant chemicals during fire fighting operations. Because fire retardant chemicals are essentially fertilizers, which are composed mainly of ammonium sulfates and (or) ammonium phosphates (Pyne et al. 1996), they are expected to cause major eutrophication effects when accidentally applied to surface waters. Although surface water bodies are avoided during aerial applications of fire retardants as mandated in the application protocols, temporary wetlands can be dry in summer and thus hardly visible from the air. In addition, adverse atmospheric conditions because of strong smoke development or wind can result in the contamination of dry, temporary wetlands. These ecosystems are not the target during fire fighting. However, recently the yearly average application of liquid concentrate of only Fire-Trol products has been ~24 000 t in North America and Mediterranean Europe (Angeler et al. 2004), which resulted in an application of ~118 000 $t \cdot year^{-1}$ of the diluted products in nature. This suggests that at least the possibility of accidental contamination of wetlands exists and calls for research related to environmental impact assessment to minimize harm in the environment when managing fires with these substances.

Environmental impact assessments regarding fire retardants in aquatic ecosystems have focused mainly on acute and chronic toxicity tests (reviewed in Giménez et al. 2004). More recently, Angeler et al. (2004, 2005*a*, 2005*b*) have studied the emergence response of populations of wetland biota from retardant-contaminated wetland soils in laboratory microcosms, and they found that the changes in water quality accounted a great deal for the emergence failure resulting in depauperate communities.

Although ecological impacts of retardant contamination can be important in wetlands, several physical, biological, and chemical mechanisms are suggested in the literature to efficiently transform contaminants of many kinds in wetlands, and these mechanisms can potentially mitigate impacts (e.g., DeBusk and DeBusk 2001). Therefore, it is necessary to determine impact-recovery patterns over multiple hydrological cycles in the field to better understand biological responses to fire retardant stress in the environment, thereby contributing to an improved environmental impact assessment and management. Employing a replicated (multiple) before–after control–impact (MBACI) design, we used artificially constructed ponds to study the impact-recovery patterns of wetland water quality. If fire retardants contribute to a sustained impoverishment of the abiotic habitat quality at the local scale, then potential effects of regional processes as influenced by landscape characteristics could reduce overall ecosystem resilience.

Material and methods

Artificial ponds

Nine cone-shaped (diameter = 4 m, depth (Z_{max}) = 1 m) ponds were constructed in the Quintos de Mora Range Station (Toledo, Central Spain) in June 2002. The ponds were spaced 4 m apart and lined with black pond foil (0.2 cm thickness) to retain water in the ponds. Thus, water loss from the ponds was exclusively by evaporation. Each pond was filled with 4000 L of water obtained from a nearby stream and transported with a tank truck. To accelerate biotic community dynamics in the ponds, sediments obtained from the Las Tablas de Daimiel National Park, a wetland included in the Ramsar convention of internationally important wetlands (Alvarez-Cobelas and Cirujano 1996), were added to the ponds and served as donor propagule banks of plant seeds and invertebrate resting eggs. These have also been used in our previous laboratory assessment studies (Angeler et al. 2004, 2005*a*, 2005*b*), which allows for cross-scale comparisons with the present study.

Sediments were collected from the uppermost layer (10–15 cm) within a 50 m × 50 m block that was homogeneous with respect to habitat characteristics (geomorphology, sediment, and vegetation characteristics). The sediment collection site was chosen because it dries out completely during summer months. The collected sediment was thoroughly mixed before application to the artificial ponds to insure homogeneity. Each pond was stocked with ~100 L of dry wetland sediment and allowed to equilibrate until March 2003 when we started the monitoring program of water quality.

When using artificially constructed ecosystems, natural environmental characteristics of real ecosystems must be simulated in a way to allow for testing a specific, ecologically relevant hypothesis. The use of natural wetland soils in our artificial ponds allowed for mimicking nutrient concentrations and biotic communities representative of a natural, protected wetland ecosystem. Many ponds occur above impermeable substrate, resulting in a negligible leaching processes and groundwater discharge. The hydrological budget of such ponds depends almost exclusively on evapotranspiration and precipitation and can result in high intra- and inter-annual water level fluctuations (Mitsch and Gosselink 2000). Because our ponds were lined with plastic, their hydrological variability reflected those of natural Mediterranean pond ecosystems (Boix et al. 2001).

Experimental retardant contamination and monitoring program

The monitoring program consisted of a retardant preapplication sampling period (Before; March 2003 – July 2003) and a postmonitoring period (After; October 2003 – May 2005). All ponds were dry between July and October 2003, and retardant was applied at the end of August 2003 to simulate a real scenario of retardant application in the field for fire fighting.

In this study, we used the commercially available fire retardant, Fire Trol® 934, obtained from ITRATECH (Gerasque, France), the European licensee for Fire Trol products in Mediterranean countries. In contrast with other Fire Trol products, the retardant used in this study lacks colour additives, which mark drop sites, and gum or clay thickeners, which increase the viscosity of the product (P. Oegema, ITRATECH, CD 46 G, 17 le Grand Sedes, F-13850 Gerasque, France, personal communication). Hence, this retardant is particularly useful for fire fighting on the ground. The liquid concentrate, which is composed >90% mass fraction of ammonium polyphosphates (the active agent in fire fighting) and only traces (<1% mass fraction) of sodium ferrocyanide (a corrosion inhibitor), was diluted with tap water to 20% volume fraction and vigorously shaken in canisters before application to the sediment surface with a knapsack sprayer. Two application rates (1 $L \cdot m^{-2}$ (Treatment 1, T1) and 3 $L \cdot m^{-2}$ (T2)) were used to experimentally contaminate ponds. These application rates were chosen to reflect manufacturers recommendations for fire fighting in grasslands and scrublands, respectively. Each treatment level was replicated three times. Three ponds were not contaminated and served as controls. Pond selection for treatment application followed a complete randomized approach.

Water quality variables were sampled in 2-week intervals during the Before period and during the first hydrological cycle of the After period. During the second hydrological cycle, samples were taken once per month. Here we define a hydrological cycle as the period spanning pond filling and drying. When ponds did not completely dry, the lowest water level within a year served to separate one hydrological cycle from the next. Field sampling included measurements of water temperature, pH, electrical conductivity, and dissolved oxygen saturation in the middle of the water column from the center of each pond. The center of each pond was accessed from a portable bridge. Water depth and Secchi transparency were also measured from the center of each pond. A depth-integrated water sample was taken from each pond center for nutrient analyses. Samples were collected in 2 L, HCl-cleaned, distilled water-rinsed PVC bottles; preserved below 4 °C during the field trip; and immediately analysed in the laboratory for contents of total nitrogen (N), ammonium, total phosphorus, soluble reactive phosphorus, chlorophyll *a*, water colour, and dissolved organic carbon (DOC). Phosphorus compounds and ammonium were analyzed according to the American Public Health Association (APHA 1989). Total N and DOC were measured in an automated N, C analyzer (Jena Analytik, Jena, Germany). Phytoplankton chlorophyll *a* was measured spectrophotometrically after extraction with 90% methanol (Marker et al. 1980). Water colour was determined spectrophotometrically according to Cuthbert and del Giorgio (1992). NH_3 data were calculated by the ammonia equilibrium equations of Emerson et al. (1975) using measured NH_4, pH, and temperature data. Hydrogen cyanide (HCN) was measured titrimetrically using the sliver nitrate method (APHA 1992, method 4500-CN D) on the first After sampling date. Because no cyanide (CN) was detected, this variable was not further analyzed on subsequent sampling dates.

Statistical analyses

Our experiment spanned sampling over periods before and after retardant contamination and was therefore suited to the BACI analytical design proposed by Stewart-Oaten et al. (1986). BACI designs have gained acceptance in environmental impact assessment because they provide the advantage to overcome problems in pseudoreplication. However, the lack of replication limits the power of BACI designs to separate treatment effects from random events. To overcome this limitation, our study involved replicate reference and treatment ponds and thus offered the opportunity for a multiple BACI (MBACI) design, suitable for repeated measures analysis of variance (RM-ANOVA; Green 1993; Paine 1996). Because most inland wetland ecosystems are highly fluctuating intra- and inter-annually, our overall approach consisted of comparing Before and After periods separately, using monthly means in the RM-ANOVA. Our null hypothesis was to detect no main effects (differences among treatment means averaged over time) and no treatment × time interactions in water quality in the Before period. However, significant time effects were expected to occur because of the drawdown over this period. By contrast, we expected significant main effects tests and (or) treatment × time interactions for most variables related to trophic state characteristics as a result of retardant contamination in the After period. Even in the absence of significant main effects tests, significant treatment × time interactions were considered indicative of changes in dependent variables that were caused by the experimental treatment (e.g., Green 1993; Paine 1996; Kreutzweiser et al. 2005). We again expected significant time effects because of the alternating flooding and drying periods that comprised the After period. To reduce the effects of multiple comparisons on the overall error rate, we adjusted *p* levels using sequential Bonferroni corrections. Planned comparisons without the necessity to adjust *p* levels were made between each Before treatment level with its respective After counterpart using one-way ANOVA to determine the magnitude of change from the Before to the After period. The data from each period and replicate pond were averaged to obtain a single value for comparisons. Because our Before period only spanned a single drying period, we checked for consistency of results using both the entire and a reduced After data set. The latter comprised data from the two drawdown periods only. Most data were log transformed, and those that contained zeros were log + 1 transformed to fulfill the requirements for parametric tests.

To determine the degree of water quality recovery after fire retardant contamination relative to the Before samples, we analyzed time trajectories using nonmetric, multidimensional scaling (NMDS). The similarity of water quality among

Fig. 1. Time course of water quality variables (means ± standard error) measured before and after experimental contamination with a fire retardant. The vertical arrow indicates when the retardant was applied to the ponds. Solid line, control ponds; dashed line, treatment 1 ponds; dotted lines, treatment 2 ponds.

Table 1. Sources in variation (*F* values) in water quality variables in experimental ponds before and after fire retardant contamination assessment using repeated measures analysis of variance.

	Before			After		
Variable	Main effects (2,6)	Time (4,24)	Interaction (8,24)	Main effects (2,6)	Time (19,114)	Interaction (38,114)
Water depth (cm)	0.1	227.0***	1.2	0.2	125.7***	0.7
Temperature (°C)	0.1	735.2***	1.1	1.3	615.6***	1.4
Secchi depth (cm)	0.0	374.3***	0.8	2.0	28.2***	1.8**
Electrical conductivity (μS·cm^{-1})	0.6	420.2***	1.7	1.9	41.5***	1.4
Water colour (mg platinum (Pt)·L^{-1})	2.2	12.5***	1.7	4.0	22.4***	0.9
pH	0.2	5.4**	1.6	3.3	18.9***	2.5**
Dissolved O_2 (% saturation)	2.7	8.5***	1.0	9.0*	93.3***	2.3**
Chlorophyll *a* (μg·L^{-1})	0.3	16.6***	1.1	21.2**	6.2***	3.9***
Total P (mg·L^{-1})	0.0	25.6***	0.6	49.9***	31.4***	7.4**
Soluble reactive P (mg·L^{-1})	0.2	8.3**	1.2	37.0***	35.4***	8.2***
Total N (mg·L^{-1})	2.5	99.3***	1.3	12.3**	24.3***	8.3***
NH_4 (mg·L^{-1})	0.0	6.5**	0.8	11.6**	23.5***	8.2**
NH_3 (mg·L^{-1})	0.3	2.7	1.8	0.5	3.0**	0.9
DOC (mg·L^{-1})	1.3	16.7***	1.3	5.6	10.5***	0.7

Note: Degrees of freedom are shown in parentheses. DOC, dissolved organic carbon; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

treatments, derived from a Euclidean distance matrix, was indicated by the proximity of points in two-dimensional scatter plots from the first two ordination axes. NMDS points for each treatment level were tracked over time in the ordination space to determine if a divergence of trends from those in the control ponds occurred after the disturbance. We averaged data from the three replicate ponds to obtain a single value per treatment and per month. The computations for all treatments were done in one analysis; however, the time trajectories are displayed in different plots for better visibility. All means were log transformed prior to analysis to down-weigh the effects of the order-of-magnitude variation of the units by which water quality variables are expressed. To determine which of the water quality variables best explained recovery patterns along the NMDS dimensions, we first reduced the water quality variables to principal factors using principal component (PC) analyses with varimax factor rotation, thereby eliminating multicollinearity between variables. Subsequently, we related the principal axes to the NMDS dimensions using Pearson correlations. All statistical analyses were run in SPSS v. 12. (SPSS, Inc., Chicago, Illinois).

Results

The high variability of Mediterranean temporary wetland ecosystems was reflected in the marked inter- and intra-annual fluctuations in all water quality variables that spanned our Before and After periods (Fig. 1). This caused the expected significant time effect for almost all water quality variables in the RM-ANOVA of the Before and After period (Table 1). Despite the high temporal variability, there were, as expected, neither significant main effects tests nor significant treatment × time interactions in the RM-ANOVAs of the Before data, suggesting similarity of water quality in all ponds.

Retardant contamination resulted in significant main effects tests and time × treatment interactions in the After period, which were highly significant for nutrients (total P, total N, NH_4, and soluble reactive P) and less significant for some other variables that depend on trophic state conditions (i.e., chlorophyll *a* and dissolved oxygen saturation) (Fig. 1; Table 1). Immediately after retardant contamination, mean total P concentration rose to 60.3 mg·L^{-1} in T1 and 216 mg·L^{-1} in T2, respectively, while pre-impact levels were maintained in the control (Fig. 1). Total N also rose to 49.3 mg·L^{-1} (T1) and 120.4 mg·L^{-1} (T2) on the first After sampling date, while the control remained at 0.56 mg·L^{-1}. The concentrations of P and N compounds tended to decrease during the After period; however, none of these variables seemed to converge with concentrations in the control during the After period. The lack of convergence was more pronounced for variables related to P compared with N compounds. The nutrient surplus seemed to have fuelled phytoplankton growth, which resulted in Chl *a* peaks of 249.2 μg·L^{-1} in T1 and 650.2 μg·L^{-1} in T2 (Fig. 1). Secchi transparency and pH showed a significant treatment × time interaction, indicating a retardant treatment effect. Electrical conductivity, NH_3, DOC, water colour, and other variables not susceptible to a change in nutrient loading (i.e., related to water depth and temperature) showed no significant treatment × time interaction (Fig 1; Table 1).

Comparisons of Before data of each treatment level with the entire data set of their After counterparts (Fig. 2) showed a significant temperature effect (i.e., the average temperature in the After period was significantly lower than in the Before period) across all treatments. Highly significant retardant effects were found for P and N compounds in both

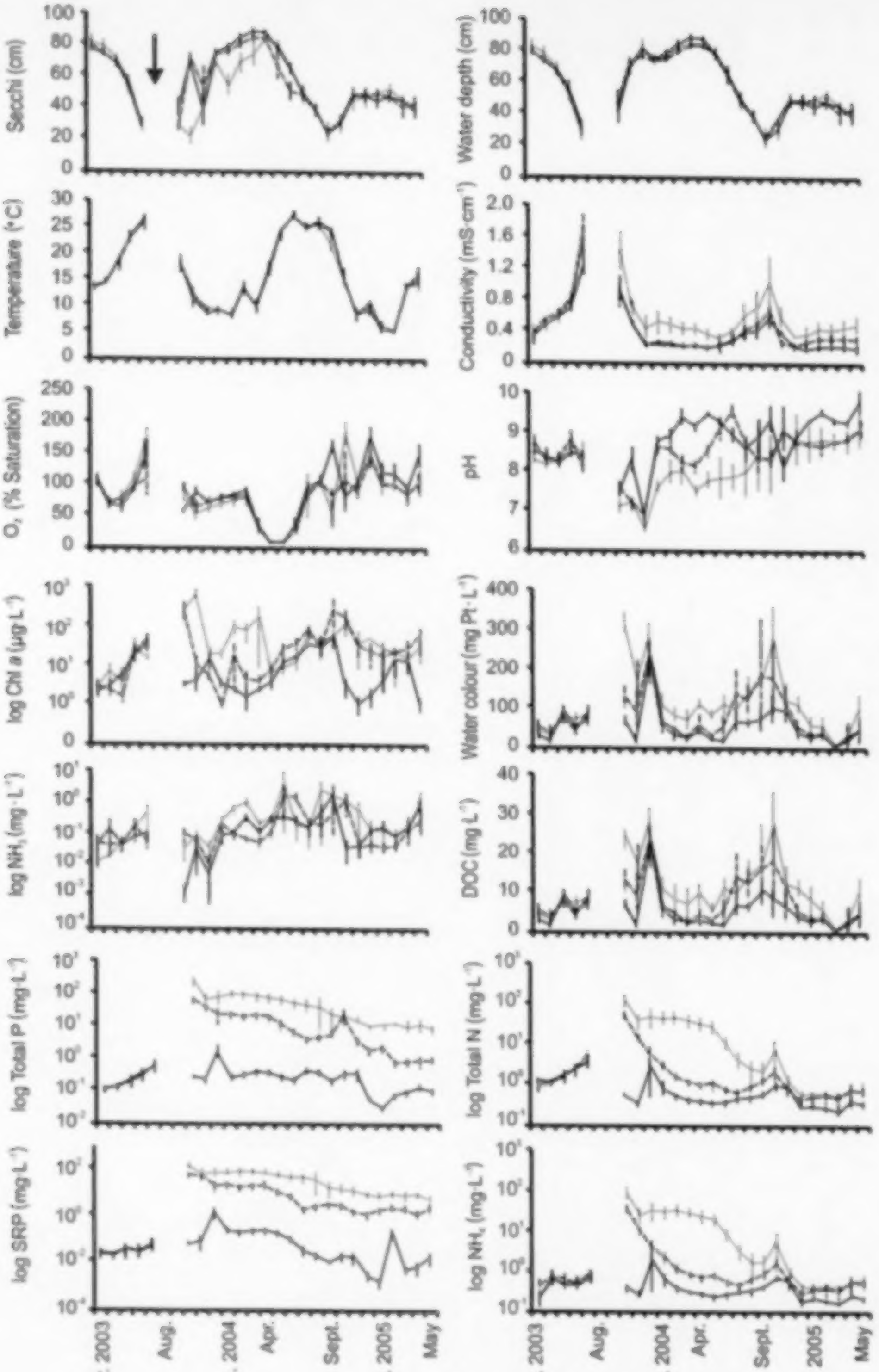
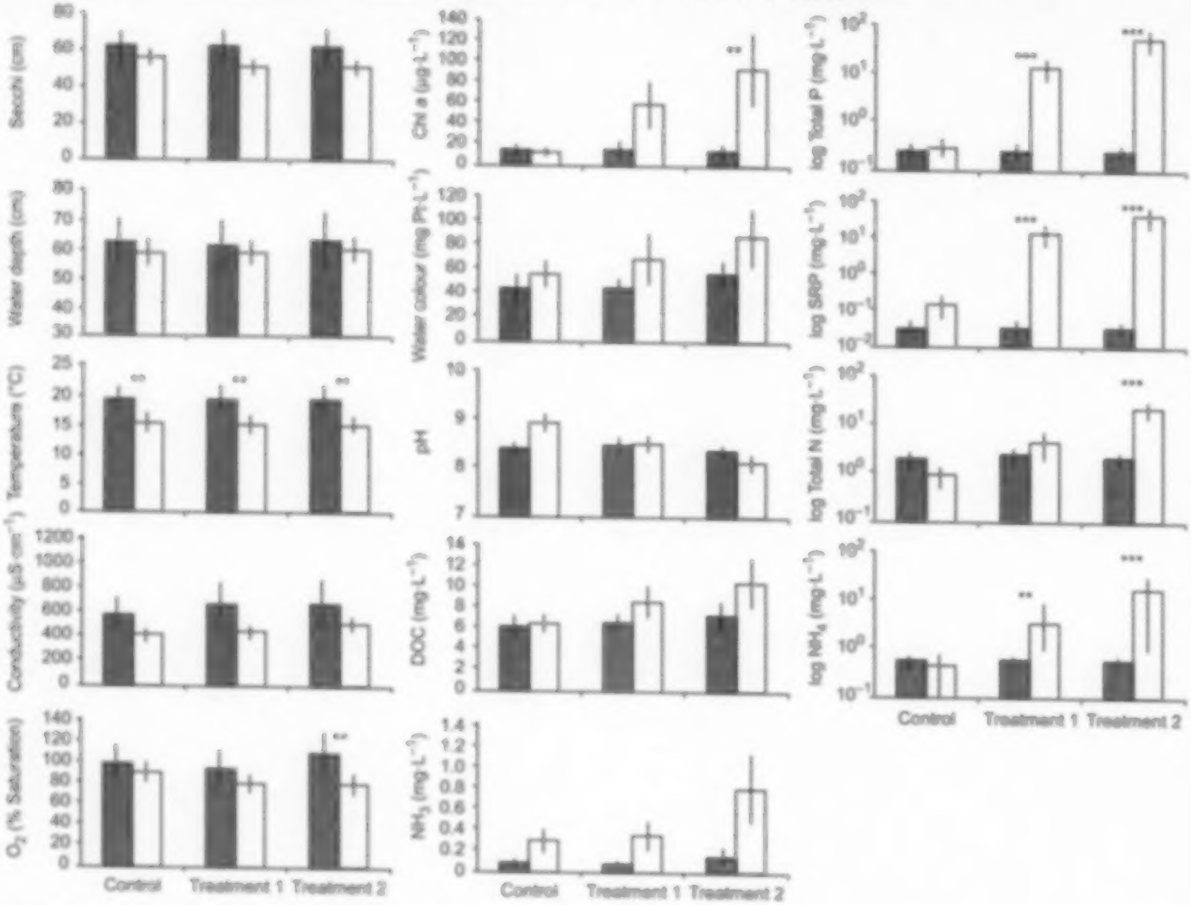

Secchi (cm)
Water depth (cm)
Temperature (°C)
Conductivity (mS·cm⁻¹)
O₂ (% Saturation)
pH
log Chl a (µg·L⁻¹)
Water colour (mg Pt·L⁻¹)
log NH₄ (mg·L⁻¹)
DOC (mg·L⁻¹)
log Total P (mg·L⁻¹)
log Total N (mg·L⁻¹)
log SRP (mg·L⁻¹)
log NH₃ (mg·L⁻¹)
Mar. 2003
Aug.
Jan. 2004
Apr.
Sept.
Jan. 2005
May
Date

Fig. 2. Comparison of water quality variables (means ± standard error) before (shaded bars) and after (open bars) experimental fire retardant contamination. Significant differences at $p < 0.01$ (**) and $p < 0.001$ (***) are highlighted.



retardant treatments, except total N, which showed no significant effect in T1. Chlorophyll *a* levels and dissolved oxygen saturation showed only significant differences in T2. Comparisons using the reduced After data set comprising only drawdown data (not shown) revealed no significant temperature and chlorophyll *a* effects. Otherwise, the results regarding nutrients and dissolved oxygen were similar to those obtained using the entire After data.

PC analyses revealed four axes, which explained 83.7% of the total variance (Table 2). PC axis 1 was composed chiefly of water quality variables related to trophic state characteristics with high factor loadings. Most of these variables were affected by the retardant (Fig. 1). PC axes 2–4 comprised variables that can vary strongly as a result of the natural, seasonal changes in ponds and that were less affected by the retardant. PC axis 2 included water depth and Secchi transparency with negative loadings and dissolved oxygen with positive loadings. Temperature and water colour comprised PC axis 3, and PC axis 4 highlights the relationship between NH_3 and pH; strong alkaline pH values favor the formation of NH_3 from NH_4.

NMDS (Fig. 3) showed that water quality of the Before and After periods overlapped in ordination space in the case of the control, but not in the case of the retardant treatments. The distance between the clouds of points from the After period relative to the Before period increased with retardant treatment along NMDS dimension 1. Pearson correlation showed a significant negative correlation of NMDS dimension 1 with PCA axis 1, which comprised trophic state characteristics (Table 3). The sampling dates in the retardant treatments showed an incomplete convergence of water quality relative to the Before and After data from the control. This suggests that water quality does not recover to preimpact conditions during the first two hydrological cycles comprising the postmonitoring period. However, T1 and T2 points were generally closer to controls in ordination space at the end of the monitoring period than shortly after the treatments, indicating some degree of recovery in the treated ponds.

The high dispersion of data points along NMDS dimension 2 was similar for the control and the retardant treatments. Pearson correlation indicated that this dimension was significantly correlated with PCA axes that reflected fluctuations in water depth, temperature, oxygen concentrations, and pH (Table 3). Thus, while NMDS dimension 1 clearly reflected anthropogenic stress as a result of retardant con-

Table 2. Summary of the varimax rotated principal component (PC) solution with correlation coefficients explaining factor loadings.

Variable	PC axis 1	PC axis 2	PC axis 3	PC axis 4
Total P	0.95			
Soluble reative P	0.93			
Total N	0.82			
NH_4	0.90			
Chlorophyll *a*	0.59			
Water depth		–0.88		
Secchi depth		–0.89		
Dissolved O_2		0.76		
Temperature			0.87	
Water colour			0.62	
NH_3				0.90
pH	–0.86			0.64
Eigenvalue	5.58	3.01	1.70	1.42
% Variance explained	39.9	21.5	12.2	10.1

Fig. 3. Nonmetric, multidimensional scaling plots showing recovery patterns of water quality in two-dimensional ordination space in the control (*a*), treatment 1 (*b*), and treatment 2 ponds (*c*). Open and solid circles represent the Before and After data, respectively. The numbers express the time trajectories in months. The stress level attained for the ordination was 0.08.

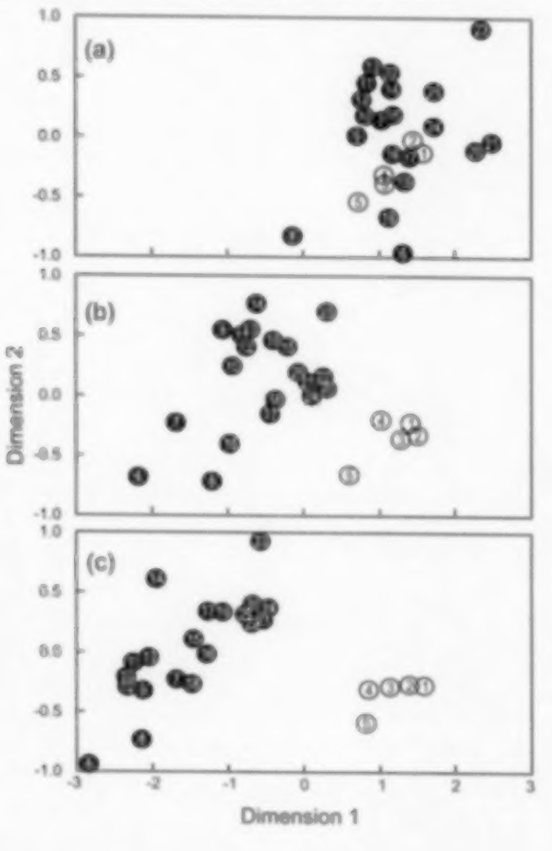


Table 3. Pearson correlation between nonmetric, multidimensional scaling (NMDS) dimensions and water quality variables that have been reduced to principal axes (see Table 2).

	NMDS 1	NMDS 2
PCA 1	–0.972	
PCA 2		–0.311
PCA 3		–0.596
PCA 4		–0.616

Note: The shown correlations were significant at $p < 0.01$.

tamination, NMDS dimension 2 was chiefly related to the seasonal variability of the ponds associated with their natural disturbance regime.

Discussion

Natural inland wetlands are highly variable in their biophysical settings, and they show gradients in size, depth, water volume, vegetation characteristics, and their hydrological connection to other surface and ground waters (e.g., Mitsch and Gosselink 2000; Euliss et al. 2004). This natural variability makes generalizations of experimental results across wetland types difficult. Therefore the impact-recovery patterns of water quality in relation to fire retardant contamination shown in our constructed ponds may show wetland-specific variation in nature. This is supported by empirical evidence. Using salt marsh and vernal pool sediments in a microcosm study, qualitative differences in water physical and chemical variables were found in response to fire retardant contamination (D.G. Angeler, unpublished data). In another microcosm study, Angeler et al. (2004) used the same sediments that served as donor soils in our ponds, and they found significant changes in electrical conductivity and water colour in addition to the variables that were affected in this study. This indicates that water volume (~100 L in the microcosms vs. >4000 L in the ponds) may have important dilution effects, thereby mediating in the qualitative impact of retardants. As has been consistently observed in this and our previous research, these products would be expected to impact on trophic state characteristics. Therefore, the results of this study are important for understanding how retardant stress can affect wetland ecosystem processes, and they have management and restoration implications.

Retardant contamination caused a significant increase in trophic state conditions. Aquatic ecosystems are classified as eutrophic above total P concentrations of ~0.03 mg·L^{-1} (Lampert and Sommer 1997). Our retardant treatment ponds surpassed this critical level at the initial After sampling dates. Although total P concentrations showed a marked decrease in the retardant-treated ponds during the post-monitoring period, total P concentrations did not drop below 2.3 mg·L^{-1} in T1 and 8.0 mg·L^{-1} in T2 by the end of the study, resulting in the persistence of the hypereutrophic state. Because the development of macrophytes was negligible in the retardant-treated ponds, we hypothesize that the marked decrease in total P could have been due to chemical binding in the sediment rather than biological uptake in plant biomass. Phosphates can bind with clays, Ca, Fe, and

Al oxides through chemisorption and form mineral compounds that are potentially very stable in the soil and afford long-term storage of P (DeBusk and DeBusk 2001). The even higher removal of N from the ponds could have included volatilization of NH_3 at pH over 8.5 and conversion of NH_4 to nitrogen gas (N_2), which is released to the atmosphere through coupled processes of nitrification and denitrification (DeBusk and DeBusk 2001).

Other studies have highlighted the formation of compounds in the water after retardant contamination that can be toxic to aquatic biota. NH_3 (e.g., Buhl and Hamilton 1998) and HCN (Calfee and Little 2003) have been considered to be the most toxic. NH_3 can form from NH_4 under conditions of high pH and water temperature, and concentrations below 1 $mg{\cdot}L^{-1}$ have been shown to be lethal to amphibians (Calfee and Little 2003) and fish (Buhl and Hamilton 1998). Fish are absent from many temporary Mediterranean wetlands, but we observed amphibian reproduction in all ponds during early spring in the Before and After period (D.G. Angeler, unpublished data), during which NH_3 concentrations were below the toxic levels reported in the literature. After completion of their aquatic life history stage, however, we observed values that surpassed these critical limits in our T2 ponds during summer months. Thus the temporal use of a habitat of sensitive fauna can be important from the toxicological risk point of view. The highest incidences of occurrence of toxic NH_3 in retardant-contaminated Mediterranean wetlands are not likely to occur during periods when amphibians reproduce.

HCN can form from sodium ferrocyanide — which is added to retardants to minimize damage to storage, transport, and delivery systems — through photoactivation when receiving ultraviolet (UV) irradiance (Calfee and Little 2003). These authors have shown a higher toxicity to fish and amphibians when fire retardants containing sodium ferrocyanide have been exposed to UV-b radiation. Because Calfee and Little (2003) measured weak acid dissociable CN, which can include the highly toxic HCN, and also metal CN complexes, which are less toxic to aquatic life (ASTM 2001), the amounts of free CN reported in their study could have been perhaps overestimated. Furthermore, these authors reported weak acid dissociable CN values in low retardant dilutions in a laboratory experiment that lasted for 24 h. Thus the extrapolation of their results to field conditions must be made with care. We did not detect free CN in our ponds at the beginning of the After period; however, the titration method used in our study does not accurately measure CN below 0.1 $mg{\cdot}L^{-1}$ (ASTM 2001). Notwithstanding methodological limitations, we do not believe that CN was a major toxic agent during our study. From the total of chemicals present in the liquid concentrate of the retardant product used here, sodium ferrocyanide occurs in less than 1% mass fraction (P. Oegema, ITRATECH, CD 46 G, 17 le Grand Sedes, F-13850 Gerasque, France, personal communication). The liquid concentrate is diluted for field application, and the resulting solution is further diluted with water upon pond filling. The use of all ponds for amphibian reproduction throughout the study provides indirect evidence for relatively low CN toxicity.

Although wetlands have frequently been considered as waste water treatment areas because they function as filters, sinks, and transformation sites for chemicals of many kinds (Kadlec and Knight 1996; Kent 2001), recent research suggest that large-scale ecosystem changes have happened in shallow lakes and wetlands that have suffered from excessive nutrient loading (Chow-Fraser 1998; Jeppesen et al. 1998; Alvarez-Cobelas et al. 2001). Shallow aquatic ecosystems can occur in two alternative stable states: the first with clear water dominated by SAV and the second with turbid water dominated by phytoplankton (Scheffer et al. 1993; Jeppesen et al. 1997; Bayley and Prather 2003). Excessive nutrient loading has been shown to be the main factor — besides water depth, herbivory, and basin slope and size — that contributes to the shift from the SAV to the degraded phytoplankton state (Moss et al. 1994; Carpenter et al. 1998; Gasith and Hoyer 1998). Our control ponds had mean chlorophyll *a* levels <20 $\mu g{\cdot}L^{-1}$ throughout the study, and the sediment surface was covered entirely by a diverse assemblage of *Chara aspera* Deth. ex Willd., *Chara hispida* L., *Chara vulgaris* L., *Ranunculus trichophyllus* Chaix, and *Zannichelia pedunculata* Reichenb., while SAV covered <10% of the pond surface (D.G. Angeler, unpublished data), and mean chlorophyll *a* exceeded 60 $\mu g{\cdot}L^{-1}$ in the retardant-treated ponds. The loss of SAV and increase of phytoplankton in our retardant-treated ponds relative to the untreated controls is consistent with a shift between alternative stable states documented in the literature. Experience from shallow, temperate, freshwater lakes suggests that substantial and sustaining recovery in the biological community in general, and vegetation characteristics in particular, cannot be expected to occur unless total P concentration has been reduced to below 0.05–0.1 $mg{\cdot}L^{-1}$ (Jeppesen and Sammalkorpi 2002). The results of our study suggest that natural wetlands may not be able to restore water quality to pre-impact levels in the short term in the absence of human intervention. Changes in water quality as a result of fire retardant contamination can maintain ecological hysteresis for at least two hydrological cycles and prevent the disruption of equilibrium conditions that trigger the return of a wetland to the clear water, SAV-dominated state.

Wildland fires and, with them, the use of fire-suppression chemicals have increased in many areas over the last decades. This is noteworthy in the Mediterranean region, in which drought and short-term heat waves appear as some of the main driving climatic variables (Pereira et al. 2005). Under climate change scenarios, these conditions are projected to dramatically increase during the 21st century (Parry 2000; Meehl and Tebaldi 2004). A parallel increment in forest fire danger conditions will take place, which is very likely to result in increased and widespread forest fire occurrences, especially large fires (Moreno 2005). Increased fire occurrence in response to climate change has already been documented in some areas of the world (Gillett et al. 2004). Temporary wetlands are abundant in Mediterranean landscapes, namely in the western part of the Iberian Peninsula, in which North Atlantic Oscillation (NAO)-controlled precipitation patterns bring abundant rainfall during fall and winter to flat and gentle-slope lands over hard bedrock, making temporary wetlands a distinguished feature of these landscapes. Owing to the poor nature of the soils, many of these areas are in a process of abandonment, thus favoring vegetation growth and, with it, fires (Moreno et al. 1998). Temporary wetlands are also a distinguished feature of the Mediterranean-type Californian chaparral shrublands (Zedler 1987; Mitsch and Gosselink 2000). Despite the biological importance of temporary wetlands in Mediterranean areas, we lack detailed inventories that would allow us to estimate how many of the areas are affected by fire and chemical fire suppression. Our results indicate that single, environmentally realistic retardant contamination events could have longer-lasting effects in wetlands, thereby compromising their ecological integrity. Fire research and suppression management should develop integral schemes to minimize ecological damage and protect ecosystem services provided by increasingly threatened temporary wetlands.

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Comparisons between hatchery and wild steelhead trout (*Oncorhynchus mykiss*) smolts: physiology and habitat use

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Abstract: Hatchery steelhead trout (*Oncorhynchus mykiss*) smolts, progeny of a newly founded native origin broodstock, were released into Abernathy Creek, Washington, in 2003 and 2004. After release, saltwater tolerance, gill $\mathrm{Na}^+,\mathrm{K}^+$-ATPase activity, and habitat use were compared. A subsample of hatchery and wild steelhead trout were implanted with 23 mm passive integrated transponder (PIT) tags each year. PIT-tagged migrants were used for physiological comparisons. Hatchery fish were significantly larger than wild fish. Hatchery migrants expressed significantly lower levels of gill $\mathrm{Na}^+,\mathrm{K}^+$-ATPase activity than wild migrants. After a 24 h seawater challenge, hatchery migrants had significantly higher plasma osmolality and $[\mathrm{Na}^+]$ than wild migrants. Microhabitat use of PIT-tagged hatchery and wild individuals in a control (wild fish only) and effect (hatchery and wild fish) site were compared before and after the introduction of hatchery fish. No difference was detected in hatchery and wild smolt habitat use. Wild fish did not change their habitat use after the introduction of hatchery fish. Although hatchery and wild fish differed in smolt physiology, differences in short-term use of freshwater habitat were not detected, and hatchery fish did not appear to displace wild fish.

Résumé : Des saumoneaux de truites arc-en-ciel anadromes (*Oncorhynchus mykiss*), issus d'une nouvelle souche reproductive indigène et élevés en pisciculture, ont été relâchés dans Abernathy Creek, Washington, en 2003 et 2004. Après la libération des poissons, nous avons comparé la tolérance à l'eau de mer, l'activité de la $\mathrm{Na}^+,\mathrm{K}^+$-ATPase des branchies et l'utilisation de l'habitat. Les deux années, nous avons implanté des étiquettes PIT (transpondeurs passifs intégrés) de 23 mm dans un sous-échantillon de truites arc-en-ciel de pisciculture et de truites sauvages. Les migrateurs munis de PIT nous ont permis de faire des comparaisons physiologiques. Les poissons de pisciculture sont significativement plus grands que les poissons sauvages. Les migrateurs de pisciculture exhibent des niveaux significativement plus bas d'activité de la $\mathrm{Na}^+,\mathrm{K}^+$-ATPase branchiale que les migrateurs sauvages. Après une exposition de 24 h à l'eau salée, les migrateurs de pisciculture ont une osmolalité plasmatique et une concentration de $[\mathrm{Na}^+]$ significativement plus élevées que les migrateurs sauvages. Nous avons comparé l'utilisation des microhabitats chez des poissons porteurs d'étiquettes PIT de pisciculture et d'origine sauvage dans des sites témoin (poissons sauvages seul) et expérimental (poissons d'élevage et d'origine sauvage) avant et après l'introduction des poissons de pisciculture. Il n'y a pas de différence d'utilisation de l'habitat entre les saumoneaux de pisciculture et les saumoneaux sauvages. Les poissons sauvages ne changent pas leur utilisation de l'habitat après l'introduction des poissons de pisciculture. Bien que la physiologie des saumoneaux soit différente chez les poissons de pisciculture et les poissons sauvages, nous ne détectons aucune différence à court terme de l'utilisation de l'habitat d'eau douce et les poissons d'élevage ne semblent pas déplacer les poissons sauvages.

[Traduit par la Rédaction]

Introduction

Hatchery smolts are increasingly being used to supplement wild populations of salmon and steelhead trout (*Oncorhynchus mykiss*) in the Pacific Northwest (Peery and Bjornn 2000). Most supplementation hatchery programs aim to minimize genetic and ecologic impacts on wild populations. The majority of work to date has examined genetic effects of hatcheries (Weber and Fausch 2003). Despite genetic similarity, in some instances juvenile hatchery fish differ physiologically, morphologically, and behaviorally from wild fish at release (reviewed by Weber and Fausch 2003). These biological differences can affect survival by contributing to individual fish interactions and interactions of fish with their

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environment. Key components of survival to adult return are adequate smolt development upon release (Zaugg 1989; Zaugg and Mahnken 1991; Beckman et al. 1999) and juvenile freshwater habitat use (Gatz et al. 1987).

Numerous studies have demonstrated that if hatchery releases are timed in concert with smolt development, survival and migration tendency are enhanced (Harache et al. 1980; Zaugg 1989; McCormick et al. 2003). Smolt development occurs in response to a combination of biotic and abiotic cues including temperature, photoperiod, and nutritional status (Grau et al. 1982; McCormick et al. 2000; Beckman et al. 2003). Often these factors differ greatly between the hatchery and wild environments.

Hatchery-reared fish released as smolts often differ in size and degree of smolt development from their wild (Leonard and McCormick 2001) or wild-reared counterparts (McCormick et al. 2003), despite their genetic similarity. In addition, genetically similar fish with differing rearing conditions have been shown to exhibit differing adult and parr phenotypes (Fleming et al. 1994; Kostow 2004) and behavior (Symons 1969; Kostow 2004) when released into the wild. These factors, as well as size (Spina 2003) and shape of fish (Bisson et al. 1988), all affect salmonid habitat use in the wild.

Water depth, velocity, substrate, and cover are critical to the distribution and abundance of juvenile salmonids (Armstrong et al. 2003). Laboratory studies show that domesticated hatchery and wild salmonids often use habitat characteristics differently (Mesa 1991; Berejikian 1994; Deverill et al. 1999). However, these studies were conducted on life stages other than smolts, and the use of these habitat characteristics changes throughout a fish's development. For this reason, the life stage at which fish are released will effect their habitat requirements and their interactions with wild fish. The majority of anadromous salmon and trout reared in the Pacific Northwest are currently released as smolts (National Marine Fisheries Service (NMFS) 2003). Despite the marked difference in physiology and behavior between the life stages and the dominance of smolt releases, there are few studies of hatchery and wild smolt interactions in the freshwater environment (for exception, see McMichael et al. 1999) and no known studies of steelhead trout smolt habitat use.

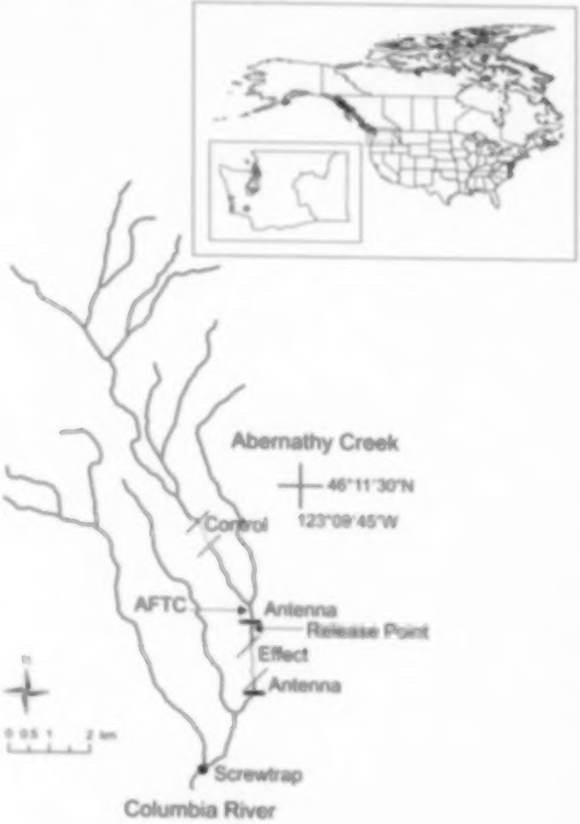
We used hatchery-reared and wild steelhead trout with the same genetic background to address several specific objectives. First, we compared the morphological and physiological characteristics of first-generation hatchery fish and their wild counterparts. Physiological changes are linked to behavioral changes (Zydlewski et al. 2005) and ultimately affect habitat use. Our second objective was to answer questions regarding hatchery and wild fish habitat use. (*i*) Of the randomly available habitat, what do hatchery and wild smolts use? (*ii*) Do hatchery and wild smolts use different habitats? (*iii*) Does the introduction of hatchery fish change the habitat use of wild fish?

Materials and methods

Study site

Abernathy Creek, a tributary to the Columbia River, in Longview, Washington, USA, is a small, third-order stream with a drainage area of approximately 110 km^2. It supports several native salmonids: steelhead trout, coho salmon (*O. kisutch*), cutthroat trout (*O. clarkii clarkii*), and chum salmon (*O. keta*) and an introduced run of fall Chinook salmon (*O. tshawytscha*).

Fig. 1. Habitat assessments and wild steelhead trout (*Oncorhynchus mykiss*) collection occurred in Abernathy Creek, Longview, Washington (noted by an asterisk (*) on the inset map). Control and effect sites were identified in 2003, electrofished in 2003 and 2004, and assessed for habitat availability in both years (shaded lines indicate site boundaries). Two stationary portable integrated transponder (PIT) tag antenna arrays were located on either end of the effect site (solid black bars). A screw trap was operated at the mouth of Abernathy Creek.



In 2003, two sections of Abernathy Creek were designated as control (wild fish only) and effect (wild and hatchery fish) sites (Fig. 1). Hatchery fish were released from Abernathy Fish Technology Center (AFTC) at stream km 3.4. The effect site was located 0.5 km downstream of AFTC and the control site was located 3 km upstream of AFTC. No hatchery fish were released upstream of the control site. The effect site was 0.5 km long and the control site was 0.8 km long (11 m mean stream width).

Fish

Wild steelhead

In the control and effect sites, five-pass electrofishing (Zippin 1958) was conducted to estimate initial density of

Table 1. Number of PIT (passive integrated transponder) and CWT (coded wire) tagged hatchery steelhead trout (*Oncorhynchus mykiss*) released per raceway (RW) in 2003 and 2004.

	RW 3		RW 4		RW 5	
	PIT	CWT	PIT	CWT	PIT	CWT
2003						
Steelhead	321	10 130	348	10 058	331	10 886
Release date	17 Apr		1 May		16 May	
Total no. released	281	10 063	304	9854	288	10 796
2004						
Steelhead	457	9811	466	9711	469	10 522
Release date	14 Apr		28 Apr		15 May	
Total no. released	405	9741	431	9668	462	10 501

juvenile steelhead trout in 2002 (10 September and 25 October) and 2003 (30 September and 29 October).

In September of 2001, 2002, and 2003, as part of another study, we captured steelhead trout larger than 100 mm fork length (FL) by electrofishing (Smith Root LR-24; Smith Root Inc., Vancouver, Washington) in the 13 km of Abernathy Creek upstream of AFTC. All individuals were tagged with a 23 mm (23 mm long, 3.4 mm wide, and 0.6 g in air) passive integrated transponder (PIT) tag. Captured steelhead trout were anesthetized with clove oil (25 ppm) and a PIT tag was inserted into the fish via an incision into the peritoneal cavity (Zydlewski et al. 2003). Capture location (to the nearest 0.5 km), FL, weight, scale samples (for aging), and a left ventral fin clip (for genetics) were collected from all individuals that were tagged. In 2001, we tagged 1099 steelhead trout. In 2002, we tagged 1360 steelhead trout, 119 in the control site and 130 in the effect site. In 2003, 2708 steelhead were tagged, 185 in the control site and 111 in the effect site. Nonlethal gill samples for Na^+,K^+-ATPase activity were collected on a subset (n = 35 per year) of fish collected from the effect site. After recovery, fish were released back into Abernathy Creek near their capture location.

Hatchery steelhead

Hatchery fish were progeny of native Abernathy Creek broodstock. Five hundred parents had been removed by electrofishing the creek and collecting young-of-the-year (0+ year class) steelhead in September of 1999 and subsequently raising them in freshwater to sexual maturity at AFTC. In late winter and early spring of 2001, 120 pairs (240 fish) were spawned as 2-year-olds. Resulting families were culled to 1000 eyed eggs to minimize family size variance. This procedure for fish collection, rearing, and spawning was repeated for brood year (BY) 2000 except that each full-sib family was culled to 350 eyed eggs. Fish were reared at an average density of 278 $fish \cdot m^{-3}$ in three concrete raceways receiving a constant flow of creek water. Raceways were covered with bird netting and had partial overhead cover. Steelhead had continual access to demand feeders and were handfed daily. In April and May of 2003 (BY 1999) and 2004 (BY 2000), 30 000 age-1+ steelhead trout smolts were released into Abernathy Creek. In each release year, fish were released by raceway in three separate groups, and the release dates occurred at 2-week intervals starting in mid-April. In both years, the first release group consisted of progeny from early in the spawning season and the final release group was from late in the spawning season.

A subset of hatchery fish were PIT tagged in January 2003 (BY 1999, n = 957) and January 2004 (BY 2000, n = 1392) when they were 163 ± 40 mm (mean ± standard deviation) FL and weighed 43 ± 26 g (Table 1). Over a 3-day period, all fish were removed from a crowded section of a raceway to a trough for coded wire tagging. In 2003, approximately every 25th fish was given a 23 mm PIT tag rather than a coded wire tag. In 2004, all fish were coded wire tagged and adipose fin clipped, and approximately every 25th fish also received a PIT tag (Table 1). Fish were monitored for tag loss and mortality during the period between tagging and release.

A subset of fish was measured (FL and weight) and gill biopsies were removed in fall, winter, early spring, and the day before release in 2003 and 2004. On each of these dates, approximately 100 steelhead were dipnetted from each raceway; from this group, we randomly selected 20 fish for sampling (size measurements and a nonlethal gill sample). Gill Na^+,K^+-ATPase activity and size data were compared among sample dates and raceways using two-way analysis of variance (ANOVA; factors: raceway and sample date).

Body size and physiology

Washington Department of Fish and Wildlife (WDFW) operated a screw trap at the mouth of Abernathy Creek from early April to mid-June in 2003 and 2004. All PIT-tagged wild and hatchery steelhead trout caught at the trap were anesthetized with MS-222 (tricaine methane sulfonate, 98 $mg \cdot L^{-1}$, buffered with sodium bicarbonate to pH = 7.0). We measured FL and weight and removed a nonlethal gill biopsy (McCormick 1993) from all PIT-tagged hatchery and wild steelhead trout captured. After recovery, fish were released downstream of the screw trap. Gill biopsies were collected into ice-cold SEI buffer (250 $mmol \cdot L^{-1}$ sucrose, 10 $mmol \cdot L^{-1}$ Na_2-EDTA, 50 $mmol \cdot L^{-1}$ imidazole, pH = 7.3), frozen on dry ice, and stored at −80 °C. Gill samples were assayed for Na^+,K^+-ATPase activity using the method of McCormick (1993).

In 2004, 3 days after each hatchery release, hatchery and wild fish (migrants) were captured at the screw trap, transferred to the laboratory (within 1 h of removal from the screw trap), and immediately exposed to seawater (32 ppt) for 24 h. The seawater challenge system consisted of duplicate circular tanks (1.2 m diameter; 710 L) connected to a chiller and pump used for recirculation. The chiller maintained water temperature between 11 °C and 14 °C. A total of three trials were conducted, each corresponding to a different hatchery release group. Hatchery and wild fish were held together in the same tank during the seawater exposure, and fish from each group were split evenly between the duplicate tanks. After exposure, fish were killed using an overdose of MS-222, and blood was collected from the caudal vein using heparinized syringes. Gill samples were collected and assayed for Na^+,K^+-ATPase activity using the method of McCormick (1993). Plasma [Na^+] was determined using an electrolyte analyzer (AVL 984; AVL Medical Instruments, Roche Diagnostics, Branchburg, N.J.), and plasma osmolality was measured with an osmometer (Osmette II; Precision Systems, Natick, Mass.).

FL, condition factor, and gill Na^+,K^+-ATPase activity of fish passing through the screw trap were compared using two-way ANOVA. All data met the assumptions of ANOVA, with the exception of 2004 gill Na^+,K^+-ATPase data. The transformation of the 2004 gill Na^+,K^+-ATPase data that met the assumptions of equal variances but violated the assumption of normality was utilized as no transformation satisfied both assumptions (per Scheffe 1959). Differences between spawning time of adults and release dates could lead to differences in fish size and gill Na^+,K^+-ATPase activity. Therefore, date (within year) was treated as a factor in the two-way ANOVA, and three blocks of time were created to correspond with each release (Table 1). Wild fish were included in the block that encompassed the date when they passed through the screw trap. Rearing type (hatchery and wild) and date (three release blocks) were the factors in the ANOVA. Plasma [Na^+] and osmolality data were analyzed with two-way ANOVA using tank and rearing type as the factors for the ANOVA.

Habitat availability

To determine habitat types available to fish, we measured physical habitat characteristics at several stratified random points throughout the control and effect sites on 28 May 2003 and 29 May 2004. Transects were positioned two mean stream widths (MSW) apart throughout the site to ensure that all habitat types were encountered (Simonson et al. 1994). In 2003, we collected habitat availability data by selecting one random location along each transect (25 transects were available per site). In 2004, we expanded the data collection method to record habitat availability throughout the season. Ten random transects were selected on each survey date and habitat measurements were recorded at one random location (randomly selected distance from the left stream bank) on each transect.

Water depth was measured to the nearest 0.1 dm. Velocity ($m \cdot s^{-1}$) was measured at 0.60 of the known water depth using an automated flow meter (model 1215; Scientific Instruments Inc., Milwaukee, Wis.). We classified the dominant substrate size at each fish detection site according to the modified Wentworth scale (Bain and Stevenson 1999). Cover was ranked on a scale of 1 to 16 according to Baltz et al. (1991). This ranking considered all possible combinations of surface turbulence, objects (i.e., debris and boulders of various size classes), rootwads, undercut banks, and overhanging vegetation. Shading was measured in µmoles using an automated light meter (model LI-250; LI-COR Inc., Lincoln, Nebraska). The light meter was positioned directly over the fish detection site (in air) so that we avoided shadowing the meter. In 2004, we recorded light readings directly above the water surface as in 2003 and at the same depth as flow measurements, 0.60 of the water depth. We categorized habitat as riffle, run, glide, or pool as described by Bain and Stevenson (1999).

To detect differences in habitat availability between the years, random habitat measurements on 28 May 2003 were compared with measurements from 29 May 2004. The two factors were year (2003 and 2004) and site (control and effect). After transformation, all data were normally distributed with equal variances.

Habitat use

In 2003 and 2004, 2 weeks before hatchery release, PITpacks (Hill et al. 2006) were used to monitor wild steelhead trout habitat use in the control and effect sites of Abernathy Creek. PITpacks are portable PIT tag detection devices that are used to scan wadeable streams in search of fish. When a tagged fish approaches the PITpack antenna or the antenna approaches a tag (within 90 cm), the PITpack beeps and records the individual PIT code. We routinely and systematically scanned the control and effect sites with PITpacks (twice before each hatchery release and twice after each release).

On each survey day, at the downstream boundary of the site, antennas of the PITpacks were submerged in the creek and tuned to the daily water conditions. Two PITpack operators then slowly moved upstream through the site scanning all available habitats. The antenna was held at a 45° angle perpendicular to water flow whenever feasible. The two operators worked through the sites, walking side-by-side, each scanning half of the creek. Fish location was considered the spot with the highest frequency of tag readings (indicated by the beeper). When a tagged fish was detected with a PITpack, we recorded the individual tag code and marked the detection site with GPS (global positioning system) and flagging. Habitat use data were collected at fish detection locations as indicated by flagging and GPS coordinates. In 2003, habitat characteristics (water depth, velocity, substrate, cover, shading) were recorded by a third observer immediately after detection. In 2004, the two PITpack operators returned at the end of the day to record habitat measurements at all detection and random sites.

To quantitatively describe hatchery and wild habitat use, we compared randomly chosen habitat availability measurements taken throughout the season in 2004 with measurements taken at detection locations of hatchery and wild steelhead trout in 2004 using one-way ANOVA (factor: detection location) with pairwise comparisons for all habitat characteristics. We transformed data to meet the assumptions of equality of variance and normality. The use of habitat types (riffle, run, glide, pool) by hatchery and wild fish were also compared using chi-square analysis. We tabulated the number of riffles, runs, glides, and pools available, as well as the number of fish detected in each of these habitats.

To determine if hatchery and wild fish differed in their habitat use, we analyzed 2003 and 2004 data using a nested ANOVA. Habitat characteristics at the position of fish detection were transformed to meet the assumption of equality of variances and normality whenever possible. In instances when normality could not be satisfied (substrate and cover), the transformation of raw data that satisfied the assumption of equality of variances was used (per Scheffe 1959). Rearing type was the fixed factor in the model and year was the random factor. Analyses that did not have a significant random effect (year) were pooled and the years were analyzed collectively (depth, velocity, and substrate). In addition, we used nonmetric multidimensional scaling ordination (MDS) to examine the habitat characteristics collectively. $\log(x + 1)$-transformed data were used because of the exponential scale of the light measurements. We used MDS rather than principle components analysis (PCA) because of the small sample sizes and nonlinearity of the data.

To detect differences in habitat use of wild fish after the release of hatchery fish, we used a before–after, control–impact (BACI) procedure. Control and impact (effect) sample data were separated into before (the first release) and after (the first release) groups by week and compared using two-way ANOVA (as described by Underwood 1992). Fixed factors included before–after groups (BA), control–impact sites (CI), and BA·CI. We treated survey week as a random, repeated measure because of the potential lack of independence between surveys. A significant BA effect indicated that fish habitat use of the two sites differed significantly during the two survey periods. A significant CI effect indicated that the use of habitat by fish differed between the sites. A significant interaction indicated that fish habitat use in the two sites was different after the release.

Fish emigration

Hatchery and wild fish were also detected moving out of the control and effect sites using stationary PIT tag interrogation systems already established on Abernathy Creek (Zydlewski et al. 2003). Systems were designed to report all detected PIT tag codes with a time stamp. Two systems were functional during the time of this study, one at AFTC (upstream of the hatchery release and effect site; downstream of all other wild fish tagging) and one approximately 1 km downstream of AFTC (downstream of all fish tagging and the hatchery release site) (Fig. 1). When used in combination, the two systems had an overall detection efficiency of 97% (91%–100%). The downstream antenna system had an antenna efficiency of 84%–97% (Zydlewski et al. 2003).

Results

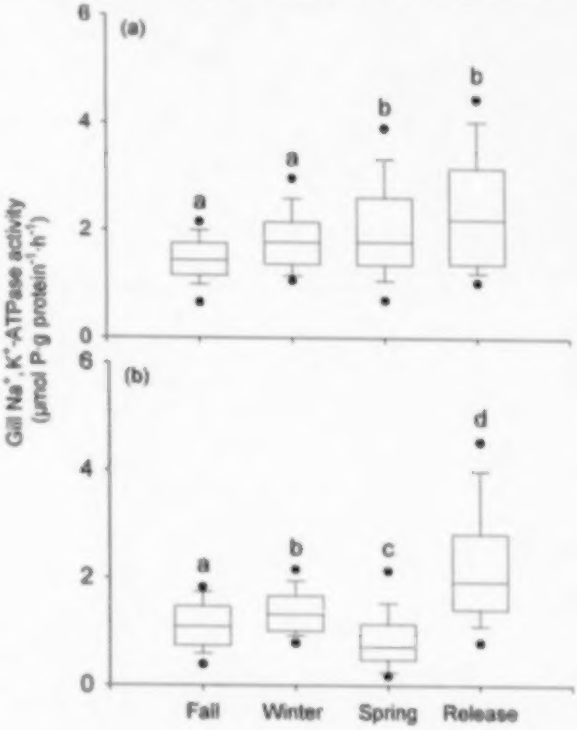
Fish

Wild steelhead averaged 129 ± 24 mm and 18 ± 13 g at the time of tagging (September and October) in 2003 and 122 ± 18 mm and 20 ± 14 g in 2004. Hatchery fish averaged 150 ± 20 mm and 36 ± 13 g at the time of tagging (January) in 2003 and 164 ± 48 mm and 27 ± 24 g in 2004.

Gill Na^+,K^+-ATPase levels in hatchery fish varied significantly throughout the year in 2003 and 2004, with the highest levels recorded in the hatchery on the day of release (Fig. 2). Differences among raceways were not significant in 2003 or 2004.

Steelhead trout density was similar in the control and effect sites before the release of hatchery fish. Wild steelhead trout density in the control site was estimated to be 6×10^{-4} fish·m^{-2} in 2003 and 5×10^{-4} fish·m^{-2} in 2004. Wild steelhead trout density in the effect site was 6×10^{-4} fish·m^{-2} in 2003 and 3×10^{-4} fish·m^{-2} in 2004. Lower densities in the effect site in 2004 were likely due to lower catch rates because of high water during sampling.

Fig. 2. Gill Na^+,K^+-ATPase activity of hatchery steelhead trout (*Oncorhynchus mykiss*) before release in April and May of (*a*) 2003 and (*b*) 2004. The line in each box represents the median, the bottom and top edges of each box represent the 25th and 75th percentiles, respectively, error bars are the 10th and 90th percentiles, and the dots indicate 5th and the 95th percentiles. Different letters indicate statistical differences ($p < 0.05$) among seasons.



Body size and physiology

Hatchery steelhead trout were significantly larger (FL and weight) than wild steelhead trout migrating during the same period in 2003 and 2004 (Table 2). In 2003, there was no difference in size among the three release blocks. In 2004, steelhead trout size did differ between the three release blocks; wild and hatchery fish captured during the first release group were significantly larger than those caught later in the season for both hatchery and wild fish (Table 2).

Gill Na^+,K^+-ATPase activity was significantly lower in hatchery fish than in wild fish in all release blocks in both 2003 and 2004 (Fig. 3; Table 2). No differences were detected among the release blocks in 2003. In 2004, hatchery steelhead trout in the first release group had significantly lower gill Na^+,K^+-ATPase than hatchery fish from the third release (Fig. 3; Table 2).

Results from the seawater challenges conducted in 2004 revealed that hatchery migrants exposed to full-strength seawater consistently had significantly higher plasma $[Na^+]$ ($P < 0.01$) and plasma osmolality ($P < 0.01$) than did wild migrants from the same trial (Fig. 4). This difference was

Table 2. Analysis of variance (rearing types are hatchery and wild; release blocks are three release dates) for fish FL, condition factor, and gill Na^+,K^+-ATPase activity for hatchery and wild steelhead trout (*Oncorhynchus mykiss*) captured at a screw trap on Abernathy Creek.

	2003			2004		
	F	df	*p*	*F*	df	*p*
Length						
Rearing type	78.3	1, 164	<0.01	58.5	1, 506	<0.01
Release block	1.59	2, 164	0.21	40.2	2, 506	<0.01
Rearing type by release block	0.31	2, 164	0.74	2.89	2, 506	0.06
Condition factor						
Rearing type	2.16	1, 164	0.14	54.3	1, 506	<0.01
Release block	1.56	2, 164	0.21	31.2	2, 506	<0.01
Rearing type by release block	2.43	2, 164	0.09	6.57	2, 506	<0.01
ATPase						
Rearing type	44.1	1, 164	<0.01	15.5	1, 506	<0.01
Release block	2.68	2, 164	0.07	10.3	2, 506	<0.01
Rearing type by release block	1.22	2, 164	0.30	0.36	2, 506	0.70

Fig. 3. Gill Na^+,K^+-ATPase activity of hatchery (open box) and wild (shaded box) steelhead trout (*Oncorhynchus mykiss*) caught in the screw trap in (*a*) 2003 and (*b*) 2004. The line in each box represents the median, the bottom and top edges of each box represent the 25th and 75th percentiles, respectively, error bars are the 10th and 90th percentiles, and the dots indicate the 5th and the 95th percentiles. Different letters indicate statistical differences ($p < 0.05$) among release blocks. Different numbers indicate statistical differences between rearing types.

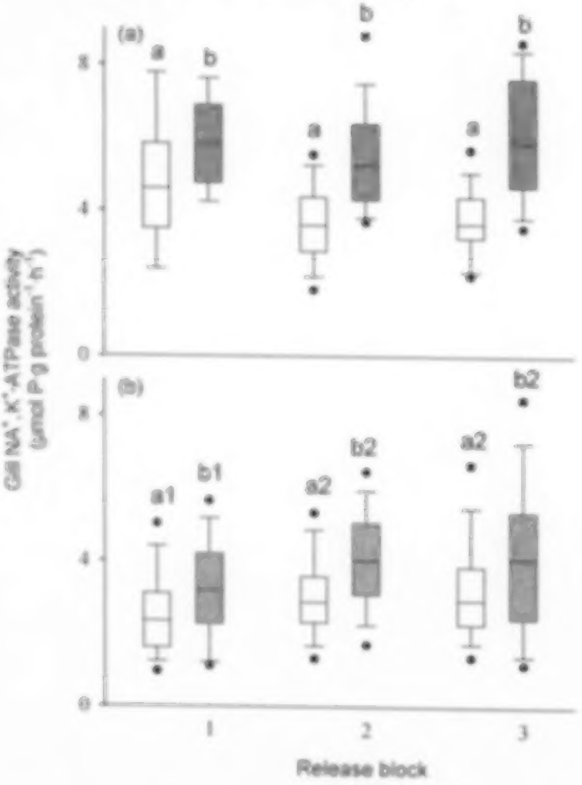


Fig. 4. Plasma (*a*) [Na^+] and (*b*) osmolality of hatchery (open box) and wild (shaded box) steelhead trout (*Oncorhynchus mykiss*) exposed to a 24 h seawater challenge. The line in each box represents the median, the bottom and top edges of each box represent the 25th and 75th percentiles, respectively, error bars are the 10th and 90th percentiles, and the dots indicate the 5th and the 95th percentiles. Different letters indicate statistical differences ($p < 0.05$) within a release block.

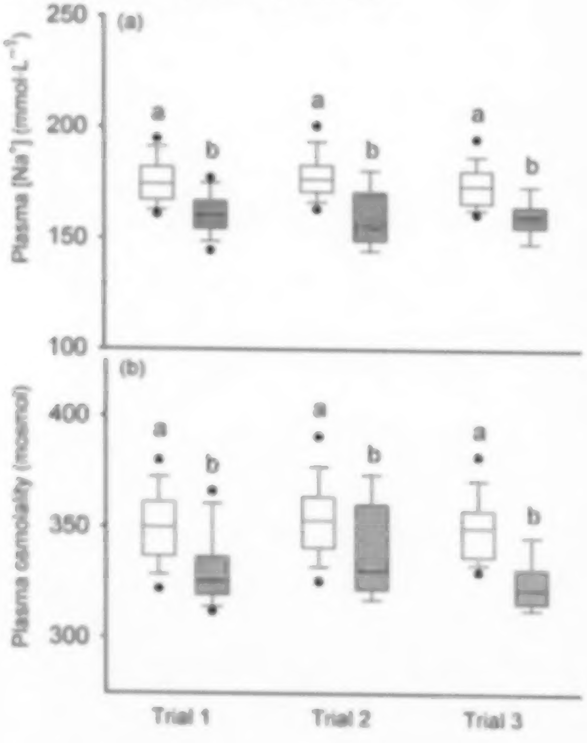
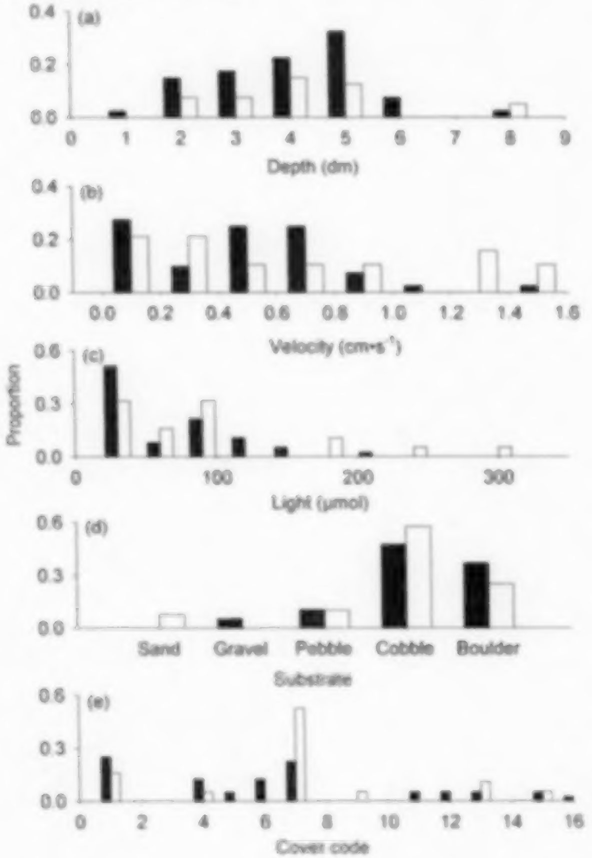


Table 3. Number of hatchery and wild steelhead trout (*Oncorhynchus mykiss*) detected in the control and effect sites in 2003 and 2004.

	2003		2004	
	Hatchery	Wild	Hatchery	Wild
Control	0	11	1	47
Effect	18	48	13*	45

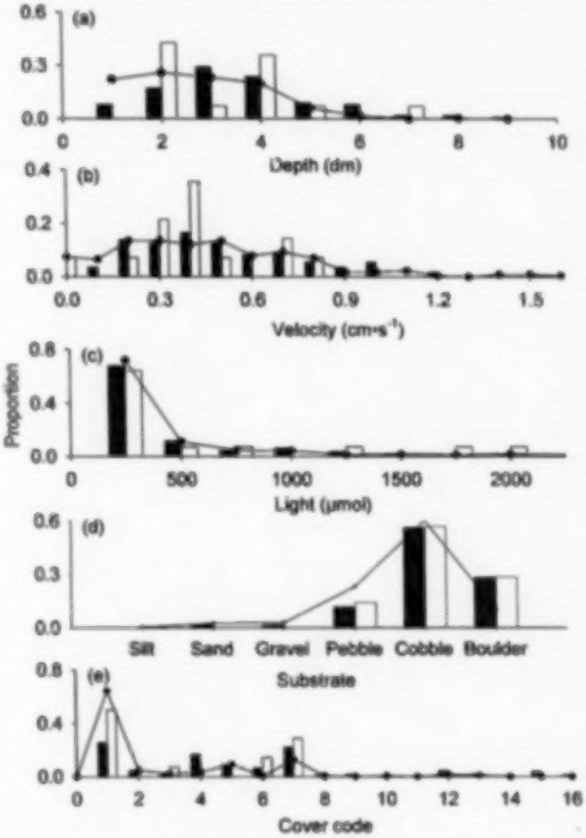
*Three of these fish were hatchery fish released in 2003 (resident hatchery fish).

Fig. 5. Distribution of habitat use for hatchery (open bar) and wild (solid bar) steelhead trout (*Oncorhynchus mykiss*) detected in 2003. Detections in each habitat class ((*a*) depth, (*b*) velocity, (*c*) light, (*d*) substrate, and (*e*) cover) are displayed as proportions of the total detections.



significant for all release blocks and did not change through the season. There was no significant tank effect for plasma [Na^+] or plasma osmolality in any of the release blocks.

Fig. 6. Distribution of habitat use by hatchery (open bar) and wild (solid bar) steelhead trout (*Oncorhynchus mykiss*) detected in 2004. Detections in each habitat class ((*a*) depth, (*b*) velocity, (*c*) light, (*d*) substrate, and (*e*) cover) are displayed as proportions of the total detections. Habitat types randomly available to steelhead trout in 2004 are indicted by a line and solid circle.



Habitat availability

The habitat available in May 2003 and May 2004 in the control and effect sites was similar. No significant differences were found in water depth, velocity, substrate, or cover. There was more shading available in the control site, when compared with the effect site, in 2003 and 2004 (F = 8.64, p = 0.005). The habitat available between years was also similar, differing only in light availability. There was significantly less shading available in 2004 compared with 2003 (F = 8.97, p = 0.004). All habitat units (riffle, run, glide, pool) were available during both years in both sites.

Habitat use

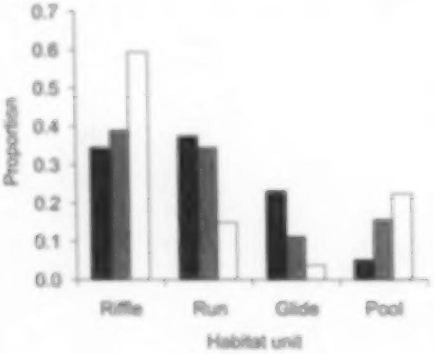
Fish were detected in all habitat types. A total of 183 individual fish were detected with PITpacks in the control and effect sites (Table 3). Fish use of the water column, substrate, and cover differed significantly from randomly available habitat. However, fish use of light and velocity did not differ from randomly available habitat. Wild fish used deeper water, larger substrate, and more cover than the randomly available habitat (Figs. 5, 6); whereas hatchery fish habitat use did not differ from the randomly available habitat (Table 4). Steelhead used riffles and pools more than were ran-

Table 4. Analysis of variance (ANOVA) for the use of habitat by hatchery and wild fish and the average habitat available.

	ANOVA		Percent difference between groups			
			Hatchery v. available		Wild v. available	
	F	*p*	Detected	Detectable	Detected	Detectable
Depth	15.0	<0.01	18	80	**29**	**8.7**
Flow	0.13	0.88	4.6	24	1.5	23
Surface light	0.30	0.74	5.2	8.1	2.4	4.2
Underwater light	0.52	0.59	8.7	306	4.5	110
Substrate	8.10	<0.01	12	29	**9.4**	**9.3**
Cover	24.5	<0.01	34	152	**94**	**55**

Note: Significant *F* values indicate that at least one group is significantly different from the others (df = 2, 351). The power analysis reveals where these differences occur and the percent difference that would be necessary to reject the null hypothesis. The percent difference between the groups detected by ANOVA is indicated in the "detected" column. The "detectable" column is the percent difference that would be required for a significant result based on the power ($\alpha = 0.05$, $\beta = 0.10$) of the performed tests, differing values for hatchery and wild fish are a result of sample sizes ($n = 15$ and $n = 100$, respectively). Significant results are in bold.

Fig. 7. Proportion of riffles, runs, glides, and pools used by hatchery (open bar) and wild (solid bar) steelhead trout (*Oncorhynchus mykiss*) compared with the habitat available (shaded bar) in 2004.

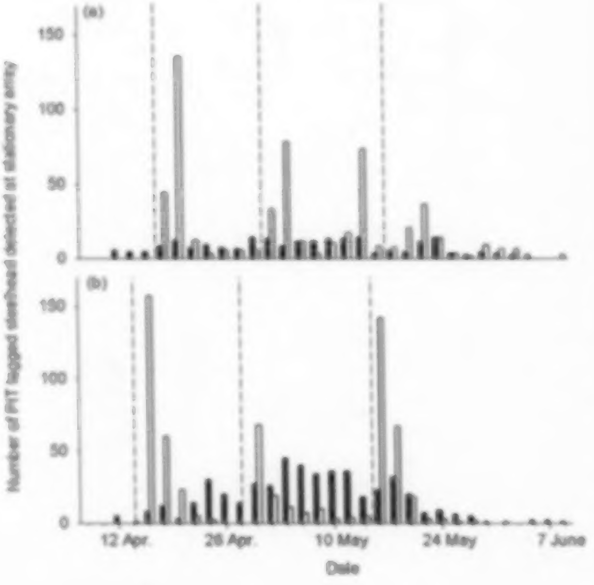


domly available, pools at levels lesser than found randomly in Abernathy Creek, and glides at similar levels as randomly available (hatchery, $\chi^2 = 182$, df = 3, $p < 0.01$; wild, $\chi^2 = 4.8$, df = 3, $p < 0.01$; Fig. 7). Hatchery and wild fish used habitat units similarly ($\chi^2 = 6.40$, df = 3, $p = 0.90$; Fig. 7).

The mean difference in velocity, depth, light, substrate, and cover use between hatchery and wild fish did not exceed 10%. However, some nonsignificant differences in the distribution of habitat use are notable (Figs. 5, 6). In 2003, 36.8% of hatchery fish were found in high-velocity (>0.7 $\mathrm{cm \cdot s^{-1}}$) habitats; 12.5% of wild fish were found at these velocities. In 2004, hatchery and wild fish used high-velocity habitats similarly. Hatchery fish were detected in six different cover combinations in 2003 and four in 2004; wild fish were detected in 10 cover combinations in 2003 and 12 in 2004. In 2003, hatchery fish were found under surface turbulence 52.6% of the time; wild fish used this cover less frequently (22.5%). Habitat differences were not evident when all habitat characteristics were considered simultaneously in the multivariate analysis, MDS ordination.

The BACI analysis did not reveal a significant change in wild fish habitat use after the release of hatchery fish relative to before release for water depth, velocity, surface light, underwater light, substrate, or cover in 2004 ($p \geq 0.16$). In addition, the main effects were not significant for any of the habitat characteristics. There was no difference in habitat use by wild fish during the before and after groups ($p \geq 0.12$) or between the control and effect sites ($p > 0.08$). High water prevented us from collecting an adequate before sample in 2003.

Fig. 8. Portable integrated transponder (PIT) tag detections of hatchery (open bar) and wild (solid bar) steelhead trout (*Oncorhynchus mykiss*) at the stationary PIT array downstream of the effect site on Abernathy Creek in (*a*) 2003 and (*b*) 2004. Vertical broken lines indicate release dates.



Fish emigration

Hatchery and wild steelhead trout were detected at the downstream stationary antenna array on Abernathy Creek (Fig. 8). In 2003, 540 hatchery and 245 wild steelhead trout were detected. In 2004, 1085 hatchery and 472 wild steelhead trout were detected. In both years, hatchery fish movement peaked the night of or day after release, whereas wild smolt movements were observed more consistently throughout the season.

Discussion

Hatchery and wild steelhead trout differed both physiologically and morphologically. Hatchery fish caught at the screw trap were larger but had lower levels of gill Na^+,K^+-ATPase activity when compared with wild fish caught at the same time. In 2004, a subsample of hatchery and wild fish caught at the screw trap were subjected to 24 h saltwater challenges. These challenges confirmed the gill Na^+,K^+-ATPase sampling results: wild fish performed better in saltwater when compared with hatchery fish, as indicated by higher gill Na^+,K^+-ATPase activity, and had better regulation of plasma $[Na^+]$ levels and osmolality. Morphometric data on the released fish reveal that hatchery fish are shaped differently than wild fish (B. Kennedy, G.B. Zydlewski, K. Ostrand, and W.L. Gale, US Fish and Wildlife Service, AFTC, 1440 Abernathy Creek Road, Longview, WA 98632, USA, unpublished data). These results are consistent with those of other studies that found that hatchery fish were larger and shaped differently than wild fish (Swain et al. 1991) and had reduced levels of gill Na^+,K^+-ATPase activity (McCormick and Björnsson 1994).

Lower levels of gill Na^+,K^+-ATPase activity and reduced seawater tolerance of hatchery fish as compared with wild fish may impact the ability of hatchery fish to survive in the ocean environment. Gill Na^+,K^+-ATPase is a membrane-bound enzyme that acts as an ion pump transferring intracellular Na^+ in exchange for extracellular K^+ ions (for reviews, see de Renzis and Bornancin 1984; McCormick 1995 and Marshall and Bryson 1998). In the developing freshwater smolt, this enzyme increases in activity in preparation for transfer to the marine environment (Zaugg and McLain 1972; Rodgers et al. 1986; McCormick et al. 2003). This increase in ATPase activity is necessary for successful osmoregulation in seawater and generally occurs in the period before and during downstream migration (Zaugg et al. 1985; Rodgers et al. 1986; McCormick et al. 2003). Several studies have linked reduced smolt survival with decreased osmoregulatory status and other indicators of smolt development such as hormone levels and migratory tendency (Zaugg 1989; Muir et al. 1994; Beckman et al. 1999). Whether the physiological differences observed in this study will translate into differences in smolt survival remains to be tested.

Size (Spina 2003) and shape (Bisson et al. 1988) can affect fish habitat use. However, the different size and shape of Abernathy Creek hatchery and wild fish did not result in consistently different habitat use. Hatchery and wild steelhead trout in this study did not differ significantly in their use of habitat characteristics (water depth, velocity, shading, substrate, and cover). Although the power of the statistical tests performed was low for determining differences in fish use of velocity, light, and cover, differences between the rearing types would have to exceed 30% for a significant result for these habitat characteristics. There was a less than 10% difference between hatchery and wild fish use of all measured characteristics. Similarly, the MDS did not reveal any clustering of hatchery and wild fish. The detected differences are small but may be biologically important and should be interpreted with caution because of the low power of the statistical tests.

Similar habitat use by hatchery and wild fish could be a function of habitat preferences or habitat availability. Hatchery and wild fish could display similar patterns of habitat use without showing a difference in habitat preference if both groups are using habitat at the same frequency as it is available. Therefore, hatchery and wild fish locations were compared with randomly available habitats of Abernathy Creek, which revealed that wild fish preferred deeper water, more cover, and larger substrate than is commonly available. Although our power to detect these preferences in wild fish was sufficiently high, our power was low for hatchery fish (because of reduced sample sizes beyond our control). The trends in hatchery (nonsignificant) and wild fish (significant) habitat preferences were similar. Therefore, hatchery and wild fish use of randomly available habitat does reveal similar habitat preferences.

When hatchery and wild fish use similar habitats, the potential for hatchery fish to displace wild fish exists (Riley et al. 2004). This is increasingly likely when hatchery fish are larger than wild fish (Rhodes and Quinn 1998), as in Abernathy Creek. No differences were found in wild fish habitat use after the release of hatchery fish. This may indicate that competition between hatchery and wild fish for habitat resources is not occurring during the days following the release of hatchery fish.

There are several possible explanations for the lack of displacement of wild fish. (*i*) Hatchery smolts are rapidly leaving freshwater and thus are not competing with wild fish. (*ii*) Hatchery and wild fish do not compete for habitat. This may occur if fish densities are low relative to randomly available habitat. (*iii*) Hatchery and wild fish do compete for habitat, but wild fish outcompete hatchery fish and thus are not displaced. (*iv*) Hatchery and wild fish are competing, but our methods did not reveal the competition.

The possibility that hatchery fish rapidly leave Abernathy Creek following release is supported by several data sources. First, detection of hatchery fish with the PITpacks was low compared with wild fish detections (23% and 13% of the fish detected were hatchery origin in 2003 and 2004, respectively). Second, stationary PIT tag antenna arrays located downstream of the hatchery release site detected large numbers of fish leaving the system within 12 h following each release (G.B. Zydlewski, M.S. Hill, W.L. Gale, and J.D. Zydlewski, unpublished data). Third, a relatively small proportion of the hatchery fish released were detected during summer PITpack surveys (after emigration should have been complete), 0.05% and 2.8% in 2003 and 2004, respectively (2.2% and 4.8% of the wild fish tagged each year were detected). Because the number of residualizing steelhead trout appears to be low, the potential impact on wild fish habitat use is also likely low. The ecological effects on the wild population from hatchery residuals cannot be dismissed and warrant further investigation.

PIT-tagged fish (hatchery and wild) were seldom found close (<1 m) together during PITpack surveys, indicating low levels of interaction between fish. Abernathy Creek's smolt production may be below its carrying capacity so that habitat availability exceeds habitat use. The carrying capacity of Abernathy Creek has not been determined, but can be approximated using the formula of Grant and Kramer (1990) (percent habitat saturation (PHS) = $100(\Sigma_{i=1}^{n} D_i + T_i)$, where D_i is density (fish·m^{-2}) and T_i is territory size). The steelhead trout density in Abernathy Creek, based on an annual smolt escapement of 4000 – 11 000 smolts (Patrick Hanratty, WDFW, 600 Capitol Way North, Olympia, WA 98501-1091, USA, unpublished data), is estimated at 0.02–0.06 steelhead trout·m^{-2}. The release of 20 000 steelhead trout smolts would raise the densities to 0.39–0.43 steelhead trout·m^{-2} downstream of the hatchery release site. Using these density values and territory sizes reported by Grant and Kramer (1990), it appears that Abernathy Creek likely remained below habitat saturation (39%–86% PHS) after hatchery releases, despite an increase in steelhead density. Therefore, it is likely that Abernathy Creek steelhead trout are not habitat-limited as a result of high fish densities. Determining a more accurate carrying capacity specific to Abernathy Creek is an important next step to the success of the native broodstock supplementation program.

The conclusion that steelhead trout are not habitat-limited is also supported by the preliminary work conducted in the control and effect sites, which shows a range of available habitat types from optimal (as indicated by wild fish presence) to suboptimal (as indicated by lack of presence). If habitat were limited, increasing use of suboptimal habitats with the increased smolt densities would be expected. A shift in habitat use was not revealed in the BACI analysis despite the range of habitats available.

If habitat were limited, a prior-residence advantage may have allowed wild fish to quickly defeat hatchery fish during competitions for optimal habitat. Support for this hypothesis from the literature is equivocal. The prior-resident effect has been demonstrated in similarly sized wild Atlantic salmon (*Salmo salar*; Huntingford and Garcia de Leaniz 1997) and hatchery and wild brown trout (*S. trutta*; Deverill et al. 1999). However, Rhodes and Quinn (1998) found that when the intruding fish was significantly larger (>6% difference) or of hatchery origin (and larger), it dominated the prior resident. We have no evidence to support competition for habitat between hatchery and wild fish at this time, although this possibility cannot be ruled out. In 2004, three "resident" hatchery fish, steelhead trout that had been released in 2003, were detected in spatially separated habitats with similar characteristics to other wild fish detection locations. With increased sampling effort and continuance of the program, it will be possible to discern whether prior residence is playing a role in the ability of wild fish to maintain their habitat. Levels of competition may increase in subsequent years as additional fish are released and remain in Abernathy Creek.

Fourth, the statistical and field methods employed may not have revealed hatchery and wild fish interactions. A power analysis of the BACI procedure revealed that power was below desirable levels for most habitat characteristics (except surface and underwater light). Low power is an issue common to unreplicated BACI designs; power can be improved with additional control or effect sites and an increase in sampling periods (Underwood 1992). A more rigorous BACI design would include multiple control sites (Underwood 1992). In this study, the control site was not replicated because of logistics. Instead, an effort was made to insure that the control and effect sites were similar for all measured parameters. Also, in 2004, the number of PIT-tagged fish, sampling effort, and performance of the PITpacks were improved to boost the sample size. Despite these improvements, the number of fish detections remained relatively constant. Detections likely remained low because the majority of smolts rapidly emigrated from the study site. Because these rapidly emigrating fish are not available for detection, increases in sampling effort may not result in significantly larger sample sizes. In addition, high levels of individual fish variation and daily variation in the stream environment make shifts in wild fish habitat use difficult to detect.

It is possible that differences between hatchery and wild fish occur on spatial and temporal scales that were not measured. Five habitat characteristics were quantified, all during the day. These characteristics were chosen because the majority of the literature recognizes water depth, velocity, substrate, and cover as critical to the distribution and abundance of salmonids (Armstrong et al. 2003). Salmonids typically seek protective habitat during the day when they are least active (Armstrong et al. 2003). As mentioned above, the availability of protective habitat may be in excess of that needed under the current densities. However, competition may still be occurring for other resources (Armstrong et al. 2003) or during the evening hours when steelhead trout are more active (Bradford and Higgins 2001). Sampling was conducted exclusively during the day because of the difficulties of employing the new PITpacks in a large stream. Day sampling methods are consistent with those of the majority of other salmonid field researchers (McMichael et al. 1999; McMichael and Pearsons (2001) included one night survey; Riley et al. 2004). PIT pack surveys during dawn and dusk may yield different results.

PIT tag technology has not previously been used to assess habitat use. Using PITpacks, habitat measurements are recorded without handling or often even viewing the fish. Because the fish is not seen at the time of detection, fish rearing type is unknown at detection and thus fish observations are unbiased. Although the technique minimizes disturbance to the fish, it creates the possibility for inaccurate habitat measurements. A rigorous comparison of habitat measurements recorded for fish detected by PITpack and more traditional methods, i.e., snorkeling, is a necessary next step. However, the PITpack method was not employed blindly. Fish were observed in an artificial stream and in Abernathy Creek to ensure that the PITpack had minimal effect on fish behavior and habitat choices (Hill et al. 2006). Results of these tests increase our confidence that the similarities between hatchery and wild fish were not due to methodology bias. In addition, if PITpacks were not detecting fish accurately in their microhabitats, no difference would be expected between the randomly chosen locations and the fish detection locations. Yet, differences greater than 10% between wild fish detected with PITpacks and the average habitat available were recorded for depth, cover, and substrate. In addition, fish were detected in areas similar to those reported for other salmonids (Armstrong et al. 2003); this would not be expected if PITpack surveys were not a viable method for quantifying habitat use.

Our result that hatchery smolts in Abernathy Creek use habitats similar to those of their wild counterparts for the short time that they reside in the creek and do not displace wild fish is important. Other studies in the months following hatchery releases have found higher levels of residualism and competition in smolts (McMichael et al. 1999; McMichael and Pearsons 2001) and differing habitat use by wild steelhead trout of earlier life stages after the release of hatchery Chinook and coho salmon smolts (Riley et al. 2004). Different hatchery rearing practices may partially explain these disparate results.

Although few details are provided about the origin of the hatchery steelhead trout used by McMichael et al. (1999), McMichael and Pearsons (2001), and the hatchery Chinook and coho salmon smolts used by Riley et al. (2004), all were supplied by WDFW hatcheries and have most likely been in captivity for more than one generation. In contrast, the Abernathy Creek hatchery fish are a first-generation native broodstock and, as a result, are genetically indistinguishable from their wild counterparts (W. Ardren, US Fish and Wildlife Service, AFTC, 1440 Abernathy Creek Road, Longview, WA 98632, USA, personal communication 2004). However, the hatchery fish were reared under traditional hatchery conditions. These differences from wild rearing conditions in some cases are sufficient to cause differences in physical attributes and behavior. Hatchery rearing of Pacific salmon in the Northwest US has become more contentious as wild stocks continue to decline. The data generated by the current study provide a useful starting point for future studies examining the role of hatchery rearing practices on the behavior, habitat use, morphology, and physiology of hatchery fish with the idea of rearing more successful smolts. Further, it will be of great interest to see if these changes to hatchery rearing practices will result in a change in the level of hatchery–wild fish interactions.

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Improving the precision of design-based scallop drag surveys using adaptive allocation methods

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Abstract: Periodic scientific surveys of commercially exploited fish and invertebrate species are a major source of monitoring data for tracking population trends and evaluating fisheries management plans. The precision of the estimates is important for assessing their quality, as well as being used directly in population models and decision rules. For design-based surveys, precision is partly a function of the survey design and can be improved for the commonly used stratified random design through the judicious definition of strata boundaries and sample-to-strata allocation schemes. In this study, we used adaptive allocation schemes to improve the precision of sea scallop (*Placopecten magellanicus*) surveys in 1999 and 2004 over the standard stratified random design. The adaptive surveys for both years were more efficient (smaller variance of the mean) than the standard stratified random surveys that had been used. Greater gains in efficiency were obtained for the 2004 survey in which scallops were more abundant (stratified mean of 227 scallops per tow) than in 1999 (stratified mean of 73 scallops per tow). The 2004 survey also benefitted from having tows allocated proportionally to stratum size at the first phase of sampling. Adaptive allocation methods appear to work best for small area surveys with one or few target species.

Résumé : Les inventaires périodiques de poissons et d'invertébrés exploités commercialement sont une source majeure des données de surveillance utilisées pour suivre les tendances démographiques et pour évaluer les plans de gestion des pêches. La précision de ces estimations est importante pour évaluer leur qualité; elles sont aussi utilisées directement dans les modèles démographiques et les règles de décision. Dans les inventaires basés sur un plan d'échantillonnage, la précision est en partie fonction du plan choisi et peut être améliorée par l'adoption, dans la méthode courante de l'échantillonnage stratifié aléatoire, de définitions judicieuses des frontières des strates et de stratégies pour attribuer les échantillons aux différentes strates. Nous utilisons dans notre étude des stratégies d'allocation adaptative pour améliorer la précision d'inventaires de pétoncles de mer (*Placopecten magellanicus*) faits en 1999 et 2004 selon le plan standard d'échantillonnage stratifié aléatoire. Les inventaires adaptatifs des deux années sont plus efficaces (variance réduite de la moyenne) que les inventaires standards stratifiés aléatoires réalisés à l'origine. L'efficacité est plus fortement améliorée dans l'inventaire de 2004 dans lesquels les pétoncles sont plus abondants (moyenne stratifiée de 227 pétoncles par trait) qu'en 1999 (moyenne stratifiée de 73 pétoncles par trait). L'inventaire de 2004 a aussi l'avantage que les traits ont été attribués de façon proportionnelle à la taille de la strate durant la première phase de l'échantillonnage. Les méthodes d'allocation adaptative semblent fonctionner mieux pour les inventaires sur de petites surfaces qui ciblent une seule espèce ou un petit nombre d'espèces.

[Traduit par la Rédaction]

Introduction

Many species of commercially exploited fish and invertebrates are monitored using periodic surveys of population numbers or biomass (Gunderson 1993). Estimates of the mean or total numbers and biomass are usually of primary interest for tracking trends or calibrating population models. However, the precision of these estimates is also of interest either for simply assessing the quality of the mean and total estimates or for actual inclusion into population models and decision rules (International Council for the Exploration of the Sea (ICES) 2004). In the latter case, increased precision of the survey estimates may lead to increased precision of model estimates.

The precision of survey means or total estimates can often be increased by using stratification, and many fish and invertebrate surveys are based on stratified sampling designs. Stratification will only provide increased precision over a simple random survey design when observations are more homogenous within strata than between strata and the samples are allocated to strata in proportion to strata size or strata variance (Cochran 1977). Gavaris and Smith (1987) evaluated the survey design for Atlantic cod (*Gadus morhua*) on the Scotian Shelf and concluded that there was more to be gained from optimizing sample allocation schemes than from stratification schemes. Similar results have been reported for Pacific ocean perch (*Sebastes alutus*) surveys (Lunsford et al. 2001), shrimp (*Penaeus duorarum* (Ault et al. 1999); *Pandalus borealis* (Folmer and Pennington 2000)), and offshore sea scallops (*Placopecten magellanicus* (Smith and Robert 1998)). On the other hand, the stratification

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schemes used for sea scallop surveys in the Bay of Fundy (Kenchington and Smith 1997) and lobster (*Homarus americanus*) trap surveys (Smith and Tremblay 2003) appeared to offer greater gains than could be realized from any potential changes to the allocation schemes.

Allocating samples in proportion to the strata variance is difficult to do before a survey is conducted unless a pilot survey is available, or if available, the variance estimates from previous years' surveys could reliably forecast the variance in each strata during the current year (Cochran 1977). On the other hand, there are a number of adaptive methods for adding samples during the survey to increase precision, and these are described in detail by Thompson and Seber (1996). Reported applications of adaptive sampling have been mainly directed towards adaptive cluster or network sampling wherein adjacent sample locations are added if the observation in the current sample meets a preset condition (Smith et al. 1995; Lo et al. 1997; Hanselman et al. 2003). In this way, sampling effort can be directed towards identifying and delineating patches of the target species. Issues have been raised concerning defining stopping rules and the resultant bias of the estimates if not all of the networks observed have been completely sampled (Lo et al. 1997; Brown and Manly 1998; Su and Quinn 2003). Unbiased estimates have been developed recently for the case of restrictions on the size of the sample (Salehi and Seber 2002).

An alternative approach to adaptive sampling is to use an adaptive allocation scheme within a stratified design. In this method, all of the strata are assigned a first-phase sample size. A second phase of random samples is added to the strata only if the appropriate conditions are met by the observations in the first phase. Although this approach will not necessarily identify patches or clusters of animals to be sampled, it can still provide an increase in precision and is unencumbered by stopping rule issues. Variants of this approach have been proposed independently by Francis (1984) and Jolly and Hampton (1990), with the merits of each approach debated in Jolly and Hampton (1991) and Francis (1991). The estimators of the mean proposed by each of the above authors have been shown to be biased (Thompson and Seber 1996).

In this paper, we present the results of applying adaptive allocation to two surveys of scallops in the Bay of Fundy. Results from attempts to optimize the allocation scheme for scallop surveys in this area based on previous surveys were mixed; therefore, an in-survey approach developed by Thompson and Seber (1996) with unbiased estimators for the mean and variance was used. In addition, we also present an estimate of the simple random sample variance of the mean from the adaptive sample that allows us to evaluate design efficiency for adaptive allocation survey designs.

Methods

Survey design

Drag surveys for monitoring scallop grounds have been conducted by the Department of Fisheries and Oceans in the Digby area of Nova Scotia since 1981. Since 1989, the survey has been conducted by the Canadian Coast Guard Cutter *J.L. Hart* with a four-gang gear using Digby drags. The stratification scheme was standardized in 1989 to represent historical areas of similar commercial effort (Fig. 1). Sample sites for standard 8 min tows were chosen randomly within strata.

The stratified mean was estimated by taking the weighted mean over all strata (Thompson 1992):

$$(1) \qquad \bar{y}_{\mathrm{str}} = \sum_{h=1}^{H} \frac{N_h}{N} \sum_{i=1}^{n_h} \frac{y_{hi}}{n_h}$$

where n_h is the number of tows sampled in stratum h ($h = 1, \ldots, H$), $n = \sum_{h=1}^{H} n_h$ is the total number of tows sampled, N_h is the total number of possible tows in stratum h, conventionally taken to be the stratum area divided by the area covered by a standard tow, $N = \sum_{h=1}^{H} N_h$ is the total number of possible tows in the survey area, and y_{hi} is the number of scallops in tow i of stratum h.

The estimated variance of the stratified mean is also weighted by strata size:

$$(2) \qquad \hat{\mathrm{V}}\mathrm{ar}(\bar{y}_{\mathrm{str}}) = \sum_{h=1}^{H} \left(\frac{N_h}{N}\right)^2 \frac{(N_h - n_h)}{N_h} \frac{s_h^2}{n_h}$$

where $s_h^2 = \sum_{i=1}^{n_h} (y_{hi} - \bar{y}_h)^2/(n_h - 1)$ is the estimated sample variance and $\bar{y}_h$ is the sample mean in stratum h.

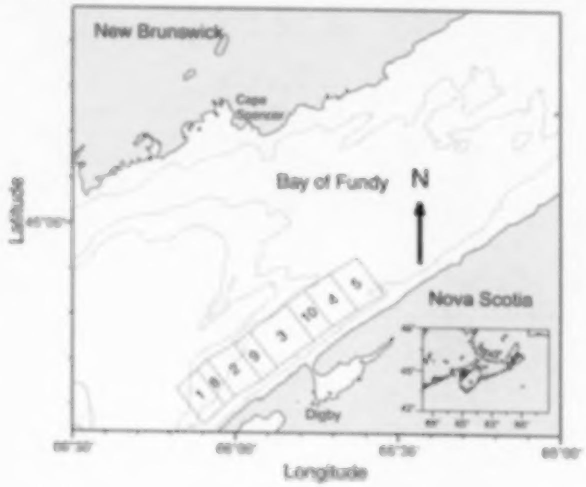
Adaptive allocation survey procedure

The rules for allocating tows to strata for most of the scallop surveys conducted from 1989 to 2004 were not explicitly designed to increase the precision of the survey estimates. In this project, the surveys in 1999 and 2004 were redesigned using the adaptive allocation scheme as described in Thompson and Seber (1996). This scheme proceeds as follows. Partition the total possible stratum sample size into $n_h = n_{1,h} + n_{2,h}$. First-phase samples ($n_{1,h}$) are allocated over the strata using some rule (past allocation, proportional to strata size, etc.). For 1999, we allocated samples to the first phase in proportion to the average stratum mean over the previous 4 years as a robust proxy for the stratum variance. In 2004, first-phase samples were allocated proportional to stratum size.

The survey was conducted for the $n_{1,h}$ sample sites over all strata. The first-phase sample mean ($\bar{y}_{1,h}$) and variances ($s_{1,h}^2$) were calculated for each stratum h based on the $n_{1,h}$ samples. Second-phase samples ($n_{2,h}$) were allocated according to some predefined decision rule (e.g., allocate second-phase samples in stratum h if the first-phase mean or variance exceeds some critical value). In most fisheries surveys, mean and variance are related, and Thompson and Seber (1996) recommended using a rule based on the first-phase stratum mean being more robust than the variance. We used stratum means for 1999 and 2004. After the second-phase samples have been chosen, the survey vessel returned to the area and conducted tows at the second-phase sample sites.

Good choices for critical values and definitions of decision rules were not investigated in this study. Past experience with this survey had indicated that some strata could be much more variable than even adjacent ones, depending on the settlement patterns of the scallops. We used a simple decision rule of adding second-phase samples only if the first-

Fig. 1. Location of strata in the Bay of Fundy, eastern Canada, used for calculation of survey indices for scallops (*Placopecten magellanicus*). Strata 1–5 and 8–10 comprise scallop production area (SPA) 4.



phase mean of commercial-sized scallops (shell height greater than 80 mm) exceeded a predefined limit, c. That is,

$$n_{2,h} = \begin{cases} n', & \text{if } \bar{y}_{1,h} > c \\ 0, & \text{otherwise} \end{cases}$$

The 1999 survey comprised a total of 85 samples allocated for the first phase with a decision rule of adding three more samples ($n' = 3$) to a stratum if the first-phase mean exceeded a threshold value of 65 commercial-sized scallops per tow. This value was based on observations from the 1998 survey.

In 2004, a total of 83 first-phase samples were allocated to strata in proportion to strata size. Five samples ($n' = 5$) were to be added to each stratum when the first-phase sample mean of commercial-sized scallops exceeded 256 scallops per tow. This threshold was based on results from a separate monitoring survey conducted in the area during June 2004. The threshold was much higher in 2004 than in 1999 because the strong 1998 year class had recruited to both the survey and the fishery.

Adaptive allocation survey estimates

The first-phase sample mean $\bar{y}_{1,h}$ remains an unbiased estimate of the population mean of stratum h even when $n_{2,h} > 0$, but it does not use data from the second-phase sampling and hence is not a function of the minimal sufficient statistic, i.e., the set of all $n_h = n_{1,h} + n_{2,h}$ distinct y_{hi} values. The mean of all n_h y_{hi} values is a function of the minimal sufficient statistic but is also a biased estimate of the stratum mean because extra samples are only added when $\bar{y}_{1,h} > c$. Thompson and Seber (1996) use the Rao–Blackwell method to develop an unbiased estimate of the stratum mean that is a function of the minimal sufficient statistic and has a variance equal to or less than the variance of the mean from the first-phase sample. In fact, because these new estimates are unbiased and based on the minimal sufficient statistic, they are also minimum variance unbiased estimators.

A general discussion of the Rao–Blackwell method is beyond the scope of this paper but the specific application to developing the estimate of the mean of the first- and second-phase samples is as follows. For strata where $\bar{y}_{1,h} > c$ and hence $n_{2,h} > 0$, compute the mean $\bar{y}_{1,hg_h}$ of the elements of each of the $G_h = \binom{n_h}{n_{1,h}}$ combinations ($g_h = 1, 2, \ldots, G_h$) of the y_{hi} values. Each combination will consist of $n_{1,h}$ observations. Let I_{hg_h} be an indicator variable such that it equals 1 when $\bar{y}_{1,hg_h} > c$ and 0 otherwise. The total number of the $\bar{y}_{1,hg_h}$ exceeding c is ξ_h. The Rao–Blackwell estimate of the mean from the first- and second-phase samples in each stratum denoted as $\hat{y}_{\mathrm{RB},h}$ is

$$(3)\qquad \hat{y}_{\mathrm{RB},h} = \begin{cases} \dfrac{1}{\xi_h}\displaystyle\sum_{g_h=1}^{G_h} \bar{y}_{1,hg} I_{hg_h}, & \xi_h > 1 \\ \bar{y}_{1,h}, & \xi_h \le 1 \end{cases}$$

In a similar manner, the variance estimate is defined as

$$(4)\qquad \hat{\mathrm{Var}}[\hat{y}_{\mathrm{RB},h}] = \begin{cases} \dfrac{1}{\xi_h}\displaystyle\sum_{g_h=1}^{G_h} \left\{ s_{1,hg_h}^2\left(\dfrac{1}{n_{1,h}} - \dfrac{1}{N_h}\right) - (\bar{y}_{1,hg} - \hat{y}_{\mathrm{RB},h})^2 \right\} I_{hg_h}, & \xi_h > 1 \\ s_{1,h}^2\left(\dfrac{1}{n_{1,h}} - \dfrac{1}{N_h}\right), & \xi_h \le 1 \end{cases}$$

where $s_{1,h}^2$ is the variance from the first $n_{1,h}$ observations and the s_{1,hg_h}^2 are the variances for the observations from each of the G_h combinations. The stratified estimates for the mean and variance of the mean analogous to eqs. 1 and 2 are as follows.

$$(5)\qquad \hat{y}_{\mathrm{RB}} = \sum_{h=1}^{H} \frac{N_h}{N} \hat{y}_{\mathrm{RB},h}$$

$$(6)\qquad \hat{\mathrm{Var}}[\hat{y}_{\mathrm{RB}}] = \sum_{h=1}^{H} \frac{N_h^2}{N^2} \hat{\mathrm{Var}}[\hat{y}_{\mathrm{RB},h}]$$

Evaluating survey designs

Survey designs are usually compared in terms of the variances of their respective means for the same total sample size. Stratified survey designs are often compared with simple random sample (SRS) designs to evaluate the gains from the allocation and stratification scheme. The survey design with the smaller variance is referred to as being more efficient. Here we compare the stratified random design for the first-phase samples and the results from the stratified random design with adaptive allocation at the second phase where additional samples are taken. Thompson and Seber (1996) define an effective sample size for adaptive cluster designs that can be used to estimate what the variance of the standard survey design would have been for the same sample size as the adaptive design. However, Thompson and Seber

Table 1. Estimates from stratified survey for scallops (*Placopecten magellanicus*; shell height ≥ 80 mm) in scallop production area 4 in June 1999.

Stratum number	Proportion of area in stratum	First phase: No. of tows	First phase: Mean number	First phase: Variance of mean	Second phase (Rao–Blackwell): No. of tows	Second phase (Rao–Blackwell): Mean number	Second phase (Rao–Blackwell): Variance of mean	Second phase (simple estimate): Mean number	Second phase (simple estimate): Variance of mean
1	0.133	14	96.9	309.2	17	105.0	257.4	105.0	257.4
8	0.068	9	119.9	514.0	12	121.6	384.0	121.6	384.0
2	0.133	19	90.7	115.6	22	93.0	116.1	93.0	116.1
9	0.100	7	71.3	90.3	10	76.0	85.8	75.7	81.4
3	0.200	17	50.7	33.7	17	50.7	33.7	50.7	33.7
10	0.100	4	65.4	565.5	7	69.4	473.1	55.6	199.9
4	0.133	8	71.7	129.8	11	71.5	96.3	69.5	77.1
5	0.133	7	32.6	163.5	7	32.6	163.5	32.6	163.5
Total	1.000	85	70.7	23.0	103	73.1	19.9	71.4	16.8

Note: An adaptive allocation scheme was used to allocate tows to strata in the second phase of the survey. The decision rule was to add three more tows if the mean in the first phase was greater than 65. The simple estimate uses the standard estimates for mean and variance for the combined first- and second-phase samples.

(1996) did not explicitly define an effective sample for adaptive allocation designs and here we simply set it to be the final sample size from the adaptive design. The variance of the stratified random mean from the first-phase samples is simply adjusted for the effective sample size assuming the same strata variances and the same allocation pattern used in the first phase.

Assuming the same strata variance estimates for the stratified random design for both the original first-phase sample size and effective sample size may not be appropriate given the small sample sizes in some of the strata. An alternate method to assess the relative gains from the first- and second-phase allocation schemes is to evaluate the variances from each phase against the estimated variance from an SRS design for the respective first-phase and total sample sizes. Given that the strata boundaries are the same for the first and second phases, the differences between the variances of the mean from the first and second phases and their respective SRS variances of the mean should be functions mainly of the differing allocation schemes and sample sizes.

The variance of the SRS mean can be estimated from the data collected from a stratified design at the first phase by using an approximate formula developed by Sukhatme and Sukhatme (1970) or an exact method given by Rao (1962). Sukhatme and Sukhatme's (1970) method is very useful because it allows for a partition of the difference between the stratified variance and the SRS variance into components due to the stratification and allocation schemes (see, for example, Smith and Gavaris 1993). As a result, the increase in efficiency due to the stratification scheme and the increase (or decrease) in efficiency due to the allocation scheme can be estimated separately. Relative efficiency results are reported here in terms of the percentage difference between the SRS and stratified variances of the mean, i.e.,

$$\frac{(\hat{\mathrm{Var}}(\bar{y}_{\mathrm{SRS}}) - \hat{\mathrm{Var}}(\bar{y}_{\mathrm{st}}))}{\hat{\mathrm{Var}}(\bar{y}_{\mathrm{SRS}})} \times 100$$

To calculate the SRS variance from the adaptive survey, we will need to develop a Rao–Blackwell version of the estimate. Unfortunately, the algebraic simplifications used in Sukhatme and Sukhatme's (1970) method to represent the allocation and stratification components complicates the development of a Rao–Blackwell estimate. The method developed by Rao (1962) gives an unbiased estimate of the SRS variance and is amenable to the Rao–Blackwell approach. The Rao–Blackwell estimate of the SRS variance of the mean from the adaptive sample is as follows (see Appendix A):

Table 2. Comparison of results from the stratified survey design after the first and second allocation phases.

	1999	2004
Variance first phase	23.0	511.7
Variance (effective sample size)	18.9	433.3
First-phase relative efficiency	13.2	7.9
Variance second phase	19.9	381.1
Second-phase relative efficiency	14.8	25.8

Note: Bay of Fundy scallop surveys in scallop production area 4 in 1999 and 2004.

$$(7)\quad \hat{\mathrm{Var}}_{\mathrm{RB}}(\bar{y}_{\mathrm{SRS}}) = \frac{N-n}{n(N-1)}\left[\frac{1}{N}\sum_{h=1}^{H} N_h \hat{y}^{2}_{\mathrm{RB},h} - \hat{y}^{2}_{\mathrm{RB}} + \hat{\mathrm{Var}}(\hat{y}_{\mathrm{RB}})\right]$$

with relative efficiency expressed as

$$\frac{(\hat{\mathrm{Var}}_{\mathrm{RB}}(\bar{y}_{\mathrm{SRS}}) - \hat{\mathrm{Var}}(\hat{y}_{\mathrm{RB}}))}{\hat{\mathrm{Var}}_{\mathrm{RB}}(\bar{y}_{\mathrm{SRS}})} \times 100$$

Results

In the 1999 survey, the first-phase sample resulted in a variance of the mean of 23.0 (relative error 6.8%; Table 1). Second-phase samples were allocated to six of the eight strata for a final total sample size of 103 (Table 1). The

Table 3. Estimates from stratified survey for scallops (*Placopecten magellanicus*; shell height ≥ 80 mm) in scallop production area 4 in September 2004.

		First phase			Second phase (Rao–Blackwell)			Second phase (simple estimate)	
Stratum number	Proportion of area in stratum	No. of tows	Mean number	Variance of mean	No. of tows	Mean number	Variance of mean	Mean number	Variance of mean
1	0.133	11	332.03	13 379.3	16	334.96	8 430.7	323.04	6 544.7
8	0.068	6	398.98	20 967.6	11	534.20	12 836.9	534.20	12 836.9
2	0.133	11	264.77	3 440.6	16	308.38	3 079.0	301.67	2 622.0
9	0.100	8	178.18	4 374.3	8	178.18	4 374.3	178.18	4 374.3
3	0.200	17	204.51	1 018.1	17	204.51	1 018.1	204.51	1 018.1
10	0.100	8	125.35	606.8	8	125.35	606.8	125.35	606.8
4	0.133	11	166.80	1 173.2	11	166.80	1 173.2	166.80	1 173.2
5	0.133	11	88.45	453.1	11	88.45	453.1	88.45	453.1
Total	1.000	83	211.46	511.7	98	226.68	381.1	224.20	339.5

Note: An adaptive allocation scheme was used to allocate tows to strata in the second phase of the survey. The decision rule was to add five more tows if the mean in the first phase was greater than 256. The simple estimate uses the standard estimates for mean and variance for the combined first- and second-phase samples.

Rao–Blackwell estimates of the stratum mean and variance are compared with simple estimates of the means and variances using all of the $n_{1,h} + n_{2,h}$ observations for each stratum. Recall, from eqs. 3 and 4, that the Rao–Blackwell estimates are based on all possible subsets of size $n_{1,h}$ of the $n_{1,h} + n_{2,h}$ total number of observations where the sample mean exceeds the threshold of 65. If all possible subsets within a stratum exceed the sample mean threshold, then the Rao–Blackwell estimates are equivalent to the simple stratum mean and variance of all of the $n_{1,h} + n_{2,h}$ observations. This was the case for strata 1, 2, and 8. For those strata where this was not so (4, 9, and 10), the simple estimates were less than the Rao–Blackwell estimates of the stratum means and variances for these strata, with the differences between the variances for stratum 10 being considerable.

The variance of the mean from the adaptive allocation scheme was 19.9 (relative error of the mean was 6.1%). The variance from the first phase corrected for the effective sample size of 103 was 18.9 (Table 2). Design efficiency for the first-phase samples using the Rao estimate in eq. 7 was 13.2%, with a simple random sampling variance of the mean equal to 26.51. For the second phase, the SRS variance decreased to 23.37, resulting in a design efficiency of 14.8% for the adaptive design.

Although the allocation scheme in 2004 could have resulted in a total sample size of 123, second-phase samples were only allocated to strata 1, 3, and 8 (Table 3). For stratum 8, all subsets of 6 tows from the total of 11 first- and second-phase tows had means that exceeded 256. As a result, the Rao–Blackwell mean and variance for this stratum were equivalent to those from the simple estimates. The first-phase sample mean and variance were 211.46 and 511.7, respectively, giving a relative error of 10.7%.

After the second-phase sample, the mean increased to 226.68, with the variance decreasing to 381.1. For comparison, the first-phase variance estimate corrected for the effective sample size was 433.3 (Table 2). Total design efficiency from the Rao estimate was 7.9% for the first phase, with a SRS variance of 555.8. The SRS variance for the second phase was 513.8, resulting in a total design efficiency of 25.8% for the adaptive allocation design.

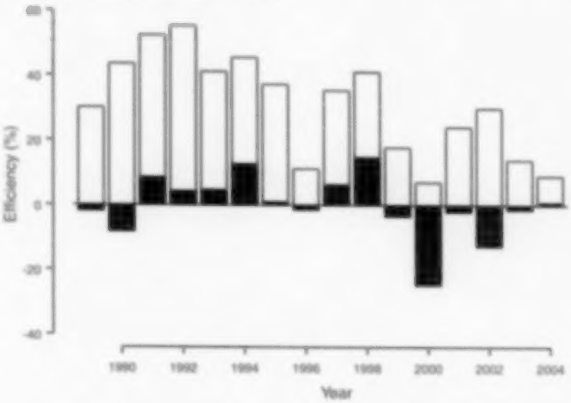


Fig. 2. Relative efficiency estimates for stratified mean number of scallops (*Placopecten magellanicus*) with shell height ≥ 80 mm from the annual scallop surveys of scallop production area 4, Bay of Fundy. The heights of the solid and open bars represent the percent efficiency for the allocation and stratification components, respectively. Addition of the heights in any one year will equal total percent efficiency. The final surveys conducted in 1999 and 2004 did use adaptive allocation designs, but the efficiency estimates presented here refer to the first-phase allocation portion of the surveys.

To put the above efficiency gains in context, we have included an analysis of design efficiency for the Bay of Fundy scallop survey estimates from 1989 to 2004. For 1999 and 2004, we only used the stratified random estimates from the first-phase samples. Using Sukhatme and Sukhatme's (1970) method, this analysis indicates that gains over SRS were mainly due to the stratification scheme (Fig. 2). The allocation scheme contributed minor increases for most years and was actually detrimental in 1989–1990, 1996, and 1999–2003. In fact, in 2000, the allocation scheme resulted in the precision of the stratified mean being less than what would have been obtained had a simple random sample design been used.

Table 4. Comparison of second-phase allocation schemes.

	1999 survey			2004 survey		
Stratum	Adaptive	Jolly-Hampton	Francis	Adaptive	Jolly-Hampton	Francis
1	3	4	3	5	7	7
8	3	2	2	5	4	5
2	3	0	0	5	3	3
9	3	2	3	0	0	0
3	0	0	0	0	1	0
10	3	5	5	0	0	0
4	3	5	5	0	0	0
5	0	0	0	0	0	0
Variance	19.9	16.3	17.3	381.1	328.3	363.9

Note: Entries are the extra number of samples allocated to each stratum. Variance refers to the variance of the mean at the second phase. Variances for the adaptive scheme are unbiased estimates, whereas variances for the other two schemes are estimated assuming that the observed first-phase variance is an appropriate estimate for the combined first- and second-phase samples.

Discussion

Comparing the first-phase stratified variance for the mean adjusted for effective sample size with the stratified variance of the mean from the adaptive allocation suggests that the final design in 1999 did not result in a gain in efficiency. However, the underlying assumption of the adjusted first-phase estimate is that it is as accurate an estimate of the population variance at the first-phase sample size (85) as it would be for the combined first- and second-phase sample size (103). If this were true, then the SRS variance after the second phase would simply be 0.83 (85/103) times the SRS variance after the first phase. However, the ratio of the estimated SRS variance after the second phase to the estimate after the first phase was 0.88, indicating that the SRS estimated variance of the mean after the second phase did not decrease as much as predicted by the increase in sample size. For this reason, the comparison of the relative design efficiency for the stratified estimates after the first and second phases is a more accurate reflection of the relative performances of the two designs. In this case, there was a marginal improvement (13.2% versus 14.8%) in design efficiency from the adaptive allocation in 1999.

Similarly, the SRS estimated variance of the mean after the second-phase allocation in the 2004 survey did not decrease as much as predicted by the increase in sample size (0.92 versus 0.85), and therefore, the first-phase variance adjusted for effective sample size underestimates the gains in efficiency from the adaptive allocation. The relative design efficiency estimates after the two allocation phases indicates that the adaptive allocation design increases the efficiency from 14.8% to 25.8%.

The lower gains in 1999 relative to 2004 may have been due to the more uniform distribution of the lower densities of commercial-sized scallops that year, which may have resulted in a negative allocation effect for the first-phase allocation (Fig. 2). Densities were much higher in 2001 and 2002 as the strong 1998 year class grew into commercial size but the allocation effect continued to be negative in those years as well. On the other hand, it is likely that simply adding three more tows in some of the strata was not enough to overcome the original poor allocation scheme. Although more tows were added per stratum in 2004, the use of allocation proportional to strata size at the first stage ensured that the second-phase allocation did not have to overcome a potentially detrimental allocation scheme at the first phase.

The annual shrimp trawl survey off of West Greenland from 1994 to 1997 was designed as an adaptive allocation survey using Francis's (1984) method. Folmer and Pennington (2000) reported that this approach was discontinued in 1998 because of concerns over the bias of the estimates of the mean and because of the additional steaming time required to add the second-phase samples. Both Francis (1991) and Jolly and Hampton (1991) discussed ways of evaluating the bias of the mean for their respective methods but assumed that the increase in precision was the main feature of the approach.

In Francis's (1984) method, extra trawl stations are added sequentially to the strata with the largest value of $N_h^2 K_h/(n_{1,h}(n_{1,h}+1))$, where K_h can be either the stratum variance or the square of the stratum mean. Jolly and Hampton (1990) allocated second-phase samples using a pseudo-optimal allocation based on first-phase variances. Application of these two approaches to our data using the square of the stratum mean resulted in very similar allocation patterns at the second phase (Table 4). This was not unexpected for the Francis and Jolly-Hampton methods given previous findings by Francis (1991) and Thompson and Seber (1996). The variance estimates in the table are for rough comparison only. The Jolly-Hampton and Francis methods use the standard estimates for stratified random designs for the combined first- and second-phase samples. These estimates are biased for these kinds of adaptive allocation designs (Francis 1984; Jolly and Hampton 1991; Thompson and Seber 1996). Further, because the data were not collected according to the above two designs, the variance estimates calculated for them assumed that the variances of the data from the first phase were adequate estimates for the combined first- and second-phase data. Experience with applying the stratified random estimates to data from the adaptive allocation design indicates that these variance estimates are likely to be underestimates (16% and 11% in Tables 1 and 3, respectively). Therefore, it is difficult to say if the allocations by both methods for the 1999 and 2004 data would have resulted in more precise designs even if unbiased estimates were available.

The Rao–Blackwell estimates presented here for the adaptive allocation design address the concern about biased estimates, and the Rao–Blackwell estimate of the SRS variance of the mean for the adaptive sample allows for evaluation of design efficiency. Although the potential increase in time required to complete the survey can be an issue for these types of surveys, this was not the case for the scallop survey. Many large scale areas such as those off West Greenland, the Grand Banks, or the Scotian Shelf are only covered once during the survey. However, the total area for scallop production area 4 only measures 618 km^2, and in the course of the day, the survey vessel could travel the length of the survey area conducting tows in conjunction with the tidal cycle. As a result, application of the adaptive survey design was no more complicated than conducting the standard survey for the same total sample size.

There is a fixed upper limit to the sample size for this kind of survey consisting of the total number of first-phase samples plus n' times the number of strata. However, this limit was never reached in the two years in which the adaptive design was used. Other areas are also surveyed in the Bay of Fundy at the same time, and effort originally scheduled for the adaptive survey was redirected to these other areas.

One limitation of the adaptive allocation type of design using any of the methods discussed here is that the decision rules are limited to a single criterion, in this case, the catch of a single target species. It may be possible to extend these rules to more than one species using one of the multi-item allocation methods discussed by Cochran (1977, pp. 119–123).

This study was not designed to evaluate the best allocation scheme for the first-phase samples, but our results support the view that if there is no information for an optimal allocation at this phase, then an allocation of samples proportional to stratum size works well. The decision rules and criterion for adding second-phase samples were based on long-term experience with this survey. Although these rules were based on the estimated mean from the first sample, we have also experimented with rules based on the proportion of tows in a stratum that contained a target species or age group (e.g., 2-year-old scallops in Robert et al. 2000). Routine use of the adaptive survey design for the Bay of Fundy scallop survey will continue, along with further investigations of decision rules and allocation schemes.

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Appendix A. Estimating variance of the simple random sample (SRS) mean from a stratified random sample.

The variance for the simple random sample mean can be expressed as follows:

$$\text{(A1)}\quad \mathrm{Var}_{\mathrm{SRS}} = \frac{(N-n)}{nN}S^2 = \frac{N-n}{n(N-1)}\left[\frac{1}{N}\sum_{h=1}^{H}\sum_{i=1}^{N_h} y_{hi}^2 - \bar{Y}^2\right]$$

where S^2 is the population variance and $\bar{Y}$ is the population mean. Rao (1962) demonstrated that

$$\text{(A2)}\quad \frac{1}{N}E\left(\sum_{h=1}^{H}\frac{N_h}{n_h}\sum_{i=1}^{n_h} y_{hi}^2\right) = \frac{1}{N}\sum_{h=1}^{H}\sum_{j=1}^{N_h} y_{hi}^2$$

Using the following relationship,

$$\begin{aligned}\text{(A3)}\quad \mathrm{Var}(\bar{y}_{st}) &= E(\bar{y}_{st} - \bar{Y})^2\\ &= E(\bar{y}_{st}^2) - 2\bar{Y}E(\bar{y}_{st}) + \bar{Y}^2\\ &= E(\bar{y}_{st}^2) - \bar{Y}^2\end{aligned}$$

and an unbiased estimate for $\bar{Y}^2$ is

$$\bar{y}_{st}^2 - \hat{\mathrm{Var}}(\bar{y}_{st})$$

where $\hat{\mathrm{Var}}(\bar{y}_{st})$ is obtained from eq. 2. Therefore, the variance of the SRS mean can be estimated from data collected in stratified random sample as follows (see also Cochran 1977).

$$\text{(A4)}\quad \hat{\mathrm{Var}}_{\mathrm{SRS}} = \frac{N-n}{n(N-1)}\left[\frac{1}{N}\sum_{h=1}^{H}\frac{N_h}{n_h}\sum_{i=1}^{n_h} y_{hi}^2 - \bar{y}_{st}^2 + \hat{\mathrm{Var}}(\bar{y}_{st})\right]$$

In a similar way, the variance of the SRS mean can also be estimated from a stratified adaptive allocation sample. Note that the first term on the right-hand side in eq. A1 corresponds to the population mean of y_{hj}^2 and that the stratified estimate of this mean is given on the left hand side of eq. A2.[1] The Rao–Blackwell estimate of this mean for stratum h is

$$\text{(A5)}\quad \hat{y}^2_{\mathrm{RB},h} = \begin{cases}\dfrac{1}{\xi_h}\displaystyle\sum_{g=1}^{G_h}\dfrac{y^2_{1,hg_h}}{n_h}I_{hg_h}, & \xi_h > 1\\ \displaystyle\sum_{i=1}^{n_h}\dfrac{y^2_{1,hi}}{n_h}, & \xi_h = 1\end{cases}$$

An estimate for $\bar{Y}^2$ can be developed as follows:

$$\begin{aligned}\text{(A6)}\quad \mathrm{Var}(y_{\mathrm{RB}}) &= E(\hat{y}_{\mathrm{RB}} - \bar{Y})^2\\ &= E(\hat{y}_{\mathrm{RB}}^2) - \bar{Y}^2\end{aligned}$$

An unbiased estimate for $\bar{Y}^2$ is provided by using the estimates in eqs. 5 and 6.

$$\text{(A7)}\quad \hat{\bar{Y}}^2 = \hat{y}_{\mathrm{RB}}^2 - \hat{\mathrm{Var}}(\hat{y}_{\mathrm{RB}})$$

Combining eqs. A5 and A7 into eq. A1, we get the Rao–Blackwell version of eq. A4:

$$\text{(A8)}\quad \hat{\mathrm{Var}}_{\mathrm{RB}}(\bar{y}_{\mathrm{SRS}}) = \frac{N-n}{n(N-1)}\left[\frac{1}{N}\sum_{h=1}^{H}N_h\,\hat{y}^2_{\mathrm{RB},h} - \hat{y}_{\mathrm{RB}}^2 + \hat{\mathrm{Var}}(\hat{y}_{\mathrm{RB}})\right]$$

PERSPECTIVE / PERSPECTIVE

Fleet dynamics and fishermen behavior: lessons for fisheries managers

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Abstract: We review fleet dynamics and fishermen behavior from an economic and sociological basis in developing fisheries, in mature fisheries near full exploitation, and in senescent fisheries that are overexploited and overcapitalized. In all cases, fishing fleets behave rationally within the imposed regulatory structures. Successful, generalist fishermen who take risks often pioneer developing fisheries. At this stage, regulations and subsidies tend to encourage excessive entry and investments, creating the potential for serial depletion. In mature fisheries, regulations often restrict season length, vessel and gear types, fishing areas, and fleet size, causing or exacerbating the race for fish and excessive investment, and are typically unsuccessful except when combined with dedicated access privileges (e.g., territorial rights, individual quotas). In senescent fisheries, vessel buyback programs must account for the fishing power of individuals and their vessels. Subsidies should be avoided as they prolong the transition towards alternative employment. Fisheries managers need to create individual incentives that align fleet dynamics and fishermen behavior with the intended societal goals. These incentives can be created both through management systems like dedicated access privileges and through market forces.

Résumé : Nous analysons la dynamique des flottes et les comportements des pêcheurs des points de vue économique et sociologique dans des pêches commerciales en émergence, des pêches en plein essor près de leur exploitation maximale et des pêches en déclin souffrant de surexploitation et de surcapitalisation. Dans tous les cas, les flottes de pêche se comportent de façon rationnelle dans les limites des structures réglementaires imposées. Les pêcheurs généralistes qui réussissent bien et prennent des risques sont souvent ceux qui initient les pêches en émergence. À ce stade, les règlements et les subventions tendent à encourager un excès de nouveaux exploitants et d'investissements, ce qui crée un potentiel pour un épuisement en cascade. Dans les pêches en plein essor, la réglementation restreint souvent la longueur des saisons, les types de bateaux et d'engins, les aires de pêche et la taille des flottes, ce qui cause ou exacerbe la course pour les poissons et l'investissement excessif; cette réglementation ne réussit généralement pas sauf lorsqu'elle est combinée à des privilèges d'accès ciblés (par exemple, des droits territoriaux et des quotas individuels). Dans les pêches en déclin, les programmes de rachat de vaisseaux doivent tenir compte du potentiel de pêche des individus et de leurs bateaux. On devrait éviter les subventions parce qu'elles prolongent la période de transition vers des emplois de rechange. Les gestionnaires de la pêche doivent créer des incitations individuelles qui ajustent la dynamique des flottes et le comportement des pêcheurs aux objectifs fixés par la société. Ces incitations peuvent être mises au point, tant par les systèmes de gestion comme les privilèges d'accès ciblés que par les forces du marché.

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Introduction

A fishery consists of two essential elements, populations of fish in their ecosystems and humans capturing the fish. It has often been noted (e.g., Wilen 1979; Hilborn 1985; Hilborn and Walters 1992) that we rarely manage the fish, and almost all regulatory action affects the fishing fleets pursuing the fish. Therefore, studying fishing fleets and their behavior should be as important a part of fisheries science as studying the ecology and population dynamics of the fish. Although the study of fish continues to dominate the funding by management agencies and the publications in scientific journals dealing with fisheries, over the last 25 years a significant literature on fishing fleets has developed.

The literature on fishing fleets is highly interdisciplinary, with publications by ecologists, economists, anthropologists, sociologists, and mathematicians. Few fisheries managers or scientists have had the opportunity to assimilate the collective knowledge regarding fishing fleets. Nevertheless, anyone involved in managing fisheries needs to be aware of the lessons of history in how fishing fleets begin, develop, and respond to regulation and closure, i.e., the dynamics of fishing fleets. The purpose of this paper is to fill this gap by reviewing the broad literature on the dynamics of fishing fleets: what determines where fishermen fish, how much they fish, how they invest in new fishing gear, and how they respond to regulation and enforcement. This field of study on fleet dynamics is essentially an analysis of the population dynamics of fishing fleets, of which there have been no reviews. Salas and Gaertner (2004) reviewed the literature on small-scale fisheries, but in this literature review we will concentrate on lessons learned from the major commercial fisheries of the world.

The universal societal goals for fisheries are to maintain healthy fish stocks to ensure sustainable fisheries, that is, to sustain the jobs, income, and food that flow from the act of harvesting fish (e.g., Pew Oceans Commission 2003). Accordingly, key words used in the Magnuson–Stevens Fisheries Management and Conservation Act include "optimum yield" and "take into account the social and economic needs of the States". Here we see the fundamental blind spot of fisheries management and policy; although the objectives are to achieve the long-term health and viability of fisheries, the prescription is to protect marine ecosystems with no words or thoughts to the dynamics of fishing fleets, including their economics and behavior. In general, fisheries management has operated under the paradigm that if you take care of the fish, you will manage fish well.

There are few formal discussions of the tradeoffs needed between different objectives in fisheries management. For instance, is the main objective to generate employment or economic efficiency? How much are we willing to overharvest less economically important species to maximize the harvest or profit from more important species? What value do we assign to commercially unimportant species such as birds and marine mammals? In the US, a few of these issues are settled in legislation such as the Endangered Species Act and the Marine Mammal Protection Act, but many other issues remain unaddressed.

We have organized this review around the cycle of fisheries development as classified by Grainger and Garcia (1996). They divided the world's major fisheries into developing, mature, and senescent, broadly displaying increasing, stable, and declining catch series; later work has suggested that 24%, 52%, and 24% of the world's fisheries fall into these three categories, respectively, and that over time, fewer and fewer fisheries will be classed as developing (United Nations Food and Agriculture Organization (FAO) 2004). During the discovery and growth phase of fisheries, the primary dynamics are the entry of new participants, the expansion of fishing capacity, and the exploration of new fishing grounds. Regulations are usually minimal during this development phase, yet during the growth phase, conditions that are set can encourage subsequent overcapitalization and economic decline. As fisheries mature, management tends to become more intrusive, limited entry is usually introduced, and stock assessments become critical. Finally, it is all too common that fleets become too large, fish become too rare, and fisheries senesce. Management actions then often include attempts at fleet reduction and rationalization, and it is important to understand how individuals and fishing fleets respond to subsidies, buybacks, and dramatic total allowable catch (TAC) reductions. During each of these phases, understanding the behavior of fishing fleets is essential to achieving reasonable long-term biological and economic management.

The problem of the race for fish

No review of fleet dynamics would be complete without at least a brief discussion of the implications of many fisheries being a common-property (or open-access) resource. Under these conditions, individuals receive all of the economic benefits of taking more of the resource (the income from fishing), while the consequences of their actions (stock depletion) are shared among all resource users, resulting eventually in the tragedy of the commons (Hardin 1968). The consequences are that fishermen (if allowed) will continue to enter a fishery as long as revenues minus costs remain above zero, until ultimately the net revenue of the entire fleet is zero — the bionomic equilibrium (Gordon 1954). At this equilibrium the resource is depleted as far as economics will allow and fishermen will move to alternative fisheries, resulting in the sequential depletion of fish stocks (e.g., Hilborn et al. 2003). Furthermore, at the bionomic equilibrium, any stock that has low harvest costs compared with revenues will be overexploited and overcapitalized or, in extreme cases, will become commercially extinct (Gordon 1954). There are wider implications of this theory, for example, reducing season length will result in a more frantic and overcapitalized race for fish (e.g., Gordon 1954; Pautzke and Oliver 1997), and adding subsidies will result in even greater overcapitalization and overexploitation of the fish stocks (e.g., Mackinson et al. 1997). The open-access race for fish, subsidies, and overcapitalization results in annual economic wastage of US$2.9 billion in US fisheries and US$60 billion worldwide (Christy 1997).

Management issues for new and developing fisheries

Few new fishing resources remain undiscovered (Hilborn et al. 2003). For those that remain, managers walk a delicate line in providing incentives that encourage the development of new fisheries while ensuring that those fisheries will be effectively managed if and when they mature. Minimizing regulatory interference will encourage individual entrepreneurs to experiment in new fisheries but may lead to an open-access situation with the attendant problems of massive increases in fishing effort and depletion of the stock (e.g., Gunderson 1984). If the regulations are cumbersome and expensive, this will tend to discourage attempts to develop new fisheries (Miller 1999). It seems reasonable to restrict the number of initial participants for a specified time period and review the progress of the fishery if catches exceed a threshold level (Boyer et al. 2001). This will ensure that the initial entrepreneurs are guaranteed a return on their investment in exploratory fishing and new gear and techniques and that depletion does not occur too soon.

In a new fishery, the rate of entry and the types of fishermen that will be attracted will depend on which fishermen think they will be better off, as predicted by standard economic utility theory. Utility theory assumes that people are rational and will attempt to maximize their happiness or satisfaction by (if possible) gaining more of whatever goods or services they desire. Bearing this in mind, we examine who enters new fisheries, how managers confront uncertainty in new fisheries, and why both biological and economic management are essential for the successful development of fisheries.

Who enters new fisheries?

Fishermen are not identical. Some will be generalists that give up some efficiency to gain the ability to fish in multiple fisheries, and others will be specialists who invest heavily in a particular fishery but cannot easily switch to another fishery (McKelvey 1983; Smith and McKelvey 1986). Both types can be active in a given fishery because generalists will be drawn into that fishery in years of high catches. Fishermen can also be divided into "stochasts" and "Cartesians" (Allen and McGlade 1986). Stochasts are willing to lead the fishery in new directions and to take risks to explore new resources, whereas Cartesians follow the leaders to exploit resources after they have been discovered. Thus stochasts may be willing to accept significant risk in exchange for high rewards, whereas Cartesians are willing to forgo occasional high returns for a steady, but lower, income.

If many different types of fishermen do exist, one would expect to see wide variation in catches among fishermen. Some (termed "highliners") would repeatedly catch large quantities of fish, whereas others would consistently obtain smaller catches. Highliners are usually stochasts and are likely to be the first people to develop new resources (Allen and McGlade 1986; Holland and Sutinen 2000). They are also likely to be generalists that are constantly exploring a range of fisheries. Over time, technology may develop to increase the efficiency (and usually the costs) of operating in that fishery, and then the specialists start to predominate; thus well-established fisheries primarily consist of specialists (Smith and McKelvey 1986). Perspectives will tend to differ among fishermen: generalists are often more focused on short-term gains relative to other opportunities, whereas specialists may be more interested in ensuring the long-term sustainability of their fishery (Smith and McKelvey 1986). The degree to which vessels and skippers each determine catching power has been debated (e.g., Pálsson and Durrenberger 1982; Hilborn and Ledbetter 1985; Squires and Kirkley 1999); however, highliners will be active in exploration whether catching power is due to vessel or skipper characteristics.

Although risk-loving behavior might be thought to be more common among fishermen exploring new fisheries, it appears to be relatively rare in the literature. This may be because it is difficult to accurately classify fishermen into the categories of risk-loving and risk-averse: fishermen may appear to be risk-loving but are actually just making bad decisions, relying on poor information, or are unlucky. When risk-loving behavior has been identified, it is generally displayed by only a portion of fishermen (e.g., Dupont 1993; Mistiaen and Strand 2000), perhaps reacting to the news of a few highly successful trips instead of average income (Holland and Sutinen 1999). Risk aversion is much more common and may contribute to a bias towards staying in the same fishery despite favorable alternatives elsewhere (e.g., Hilborn and Ledbetter 1979; Dupont 1993). However, it should be noted that high switching costs (Hilborn and Ledbetter 1979; Dupont 1993) or great uncertainty about catches outside known areas (as in the historical Swedish longline fishery; Poulsen 2005) might result in a rational response to eschew exploration.

The first entrants into a new fishery would therefore be expected to be generalists who are drawn towards opportunities with an expected high payoff, but are not necessarily risk-loving. These conclusions are, however, largely based on theory and not fisheries case studies.

Factors influencing entry and exit decisions

Entry and exit decisions in fisheries cannot be considered in isolation. Individuals may enter a fishery because it is a new fishery or as a result of spillover effects caused by the collapse of existing fisheries. There is limited literature studying these entry–exit decisions. Although numerous case studies exist about the development of new fisheries, only two studies were found that examine the relative earnings of fishermen that enter, remain in, and exit fisheries. Pradhan and Leung (2004) explored entry–exit decisions in the Hawaii longline fishery, which targets tuna and swordfish. In this fishery, earning potential, fleet size, and resource abundance affected entry–exit decisions, and fishermen were more likely to stay in the fishery if the vessel owner was a resident of Hawaii. Furthermore, annual revenue, number of trips, and days at sea was highest for those who remained in the fishery and lowest for those who exited.

Entry–exit behavior was also examined in the Gulf of Mexico shrimp fishery (Ward and Sutinen 1994). In contrast to the results of Pradhan and Leung (2004), new entrants to the fishery had the highest average catches, 1053 kg per trip, whereas those who remained in the fishery averaged 762 kg per trip, and exiting vessels averaged only 583 kg. The probability of exiting was most affected by harvesting costs and ex-vessel prices.

Culture and hierarchy also matter. In Iceland, low catches are considered to be humiliating, so leaving the fleet to explore new fishing opportunities is only possible for successful captains with close bonds to crew (Pálsson and Durrenberger 1982). The costs and benefits of search may vary for different fishermen.

The above analysis fails to really capture the "who" of a new fishery. Some evidence suggests that it is highliners, but we do not have a clear theory or pattern to explain the type(s) of fishermen expected to predominate in new fisheries. More research tracking fishermen before and after they enter a fishery is needed to better understand the particular characteristics of fishermen in new fisheries.

The role of uncertainty in managing developing fisheries

Managing and tolerating uncertainty is a key aspect of fishery management. What happens depends on biology, economics, and management institutions. How one controls access will clearly have large effects on what happens in a fishery. Hilborn and Sibert (1988) found that most fisheries do not have the institutional capacity to restrict fishing effort when necessary, an essential component of effective management.

New fisheries may develop from a sideline fishery, previously discarded bycatch, or from fish previously unknown to fishermen. Technology may also be developed or imported that makes a particular type of fishing or processing viable (e.g., US West Coast shrimp processing). New species may also be added to a suite of fishable species, as in the US West Coast trawl fishery (Gunderson 1984), which may change the dynamics of the fishery to encourage new entry and present new management challenges. For bycatch and sideline fisheries, managers should assess what conditions changed to cause the fishery to be targeted: have the market conditions changed for the previously nontargeted fish or is this stock part of a process of sequential depletion? If a new stock is "found" or "discovered", as stocks of orange roughy (*Hoplostethus atlanticus*) and swordfish (*Xiphias gladius*) commonly are, a different set of conditions may apply. The fishery may be extremely valuable and could suffer rapid and irreversible depletion if it is not carefully regulated.

Many factors drive the degree to which fishermen will enter a fishery as it develops. Available capital and fishing equipment, knowledge about the fishery and the institutions that govern it, and market conditions for the fish will all affect entry. There may be investment lags between the decision to enter and actually entering the fishery, and in some cases, the initial years may be unprofitable (Pradhan and Leung 2004). However, one has to carefully weigh these investment trade-offs with the benefits of capturing rents (economic returns that exceed the minimum required to induce entry to a fishery) in a newly developing fishery. The first entrant in a new fishery may develop highly profitable, near-monopoly power if the demand for the fish is strong. Given the depleted condition of many existing fisheries, it is more likely that a developing fishery will experience a rapid influx of new entrants, thus the survival of a fishery often depends on swift action well before any signs of stock decline emerge (Walters 1998).

Several examples illustrate how quickly fisheries can decline. The Namibian orange roughy fishery expanded and declined within 6 years (Boyer et al. 2001). The story of this fishery is not one of inattention, but rather highlights the problems of uncertainty and optimistic interpretations of the biological state of the fishery. The fishery followed "best practices", but managers did not pay adequate respect to uncertainty in all aspects of management, which led to the rapid decline of the fishery. With a long-lived species such as orange roughy, recovery will be extremely slow and the overly optimistic management of the fishery was costly.

Widow rockfish (*Sebastes entomelas*) on the US West Coast are another example of how one can "miss the boat" in a very short period of time. Excessively optimistic interpretations of data led to the collapse of this fishery in just 3 years and therefore "imprecise assessments necessitate course controls, with ample protection against damage to the resource base from overharvesting" (Gunderson 1984). Subsidies for new boats combined with declining alternative stocks and nonscientific allowable catch levels contributed to overfishing and rapid exhaustion of the widow rockfish fishery.

Managing both the biology and economics of new fisheries

Many new fisheries have included an initial period in which managers made concerted efforts to understand the biology of the fish being exploited. What has almost always been missing from this period, however, is an effort by managers to control the economics of the fishery. The key point here is that even if a fishery is managed ideally from a biological perspective, most of its benefits will be squandered if the fishery operates under open-access conditions.

Exploratory fishing often results in lower catch rates (e.g., Rijnsdorp et al. 2000). If fishermen knew that they would have greater catch by exploring, they would explore all of the time instead of continuing to fish in known grounds. However, because open access leads to rent dissipation in established fisheries, new fisheries present the best opportunity for fishermen to capture positive resource rents.

The wreckfish (*Polyprion americanus*) fishery in the southeastern US provides an example of how management can fail both biologically and economically, leading to the benefits of a fishery being lost to open access. The wreckfish fishery was discovered when swordfish longliners were recovering pieces of pelagic longline gear (Gauvin et al. 1994). From 1987 to 1990, the wreckfish fishery expanded from less than 13.6 t to 1800 t, and the fleet grew from two to more than 20 vessels. An intense derby-style fishery in 1990 resulted in the entire TAC being caught within 2 months. Prices plummeted because of the resulting glut of product on the market. In 1992, individual transferable quotas (ITQs) were implemented and the severe open-access problems were addressed (Gauvin et al. 1994). However, the implementation of ITQs did not solve all the problems in the fishery because the TAC was set too high and overfishing continued up to 1994, leading to declining catch rates, and as a result, the catches decreased steadily to 10% of the allowable quota in 1998 (Vaughan et al. 2001). Given the long reproductive lives of wreckfish and uncertainty about their population status, it is unclear whether or not the population is currently being overfished, despite low catch levels. During the short time when there was a strong market for wreckfish and high catch rates, many of the rents were lost because of open access. Despite belated attempts to be biologically responsible, a failure to quickly address the economic problems and to conservatively assess the biological potential of the fishery led to the loss of most of the possible economic gains from the fishery. Although ITQs can much better capture the economic benefits of a fishery, ITQs cannot revive a severely depleted fishery, nor can they ensure that favorable market conditions will continue.

Implications of fishermen behavior in the management of new fisheries

In summary, a relatively limited amount of research has been conducted about entry–exit behavior in fisheries, and little empirical analysis has been conducted about what types of fishermen enter new fisheries. Nevertheless, we can suggest a number of practical rules for managing new and developing fisheries.

Joint biological and economic management is crucial when starting a new fishery. It is insufficient to aim solely for biological sustainability at the start of a fishery, because there is great uncertainty about what catch levels will be sustainable, and because a rapid buildup in the fleet size could swiftly deplete the fish stock. Conversely, it is insufficient to aim solely at maximizing economic benefits from the fishery, because in some cases, the greatest benefits are obtained by rapidly depleting the stock (e.g., Clark 1973), and legal mandates for conservation render this option unacceptable. Instead, managers of new fisheries should concentrate on controlling both fishing mortality and fishing capacity to ensure biological and economic sustainability.

Research about the fishermen involved in new fisheries also has several implications. Fishermen exploring new fisheries are likely to be generalists and highliners who are more willing to tolerate risk than other fishermen. Managers of new fisheries might therefore reasonably focus their attentions on a limited class of fishermen most likely to participate in new fisheries. The risk of economic overexploitation (i.e., wasteful overcapitalization) will increase when there are few alternative fisheries and large amounts of latent fishing capacity suited for generalist fishing. The risk of biological overexploitation will be highest when the species is valuable, costs little to exploit, is easily caught, and is both long-lived and slow-growing.

Unfortunately, fisheries have a long history of sequential depletion, readily evident in the history of whaling, in which fishermen focused on increasingly less commercially valuable species of whales (Hilborn et al. 2003). Rapid responses to the development of new resources are necessary to prevent fishermen from repeating this pattern throughout the world's fisheries.

Mature or established fisheries

In established fisheries, managers tend to concentrate on how to assess the status of the stocks and how to control fishing effort. In many fisheries, attempts have been made to control fishing effort by restricting season length, vessel and gear types, and fishing areas and by limiting the number of boats. These options generally cause or exacerbate a race for fish and excessive investment. Managers and researchers have therefore displayed considerable interest in alternative management systems such as granting dedicated access privileges to specific user groups.

Fisheries stock assessments

In all stages of fisheries development, but perhaps particularly in established fisheries, stock assessments are used to estimate the current status of fish stocks. Typically, stock assessments rely on a combination of information obtained from fisheries, such as commercial catch-per-unit-effort (CPUE) indices, catch length frequencies, and catch-at-age data, and fisheries-independent data obtained from standardized trawl or acoustic surveys. Clearly fleet dynamics and fishermen behavior do not affect fisheries-independent surveys or the data they produce, thus we concentrate on their influence on commercially obtained data.

Commercial length and age frequencies

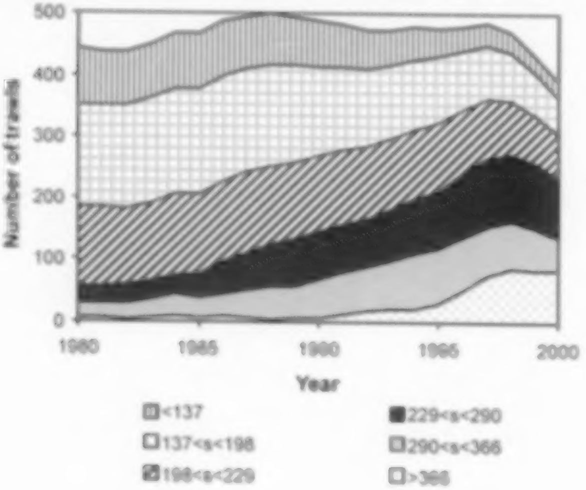
Length and age frequencies are most useful if they are representative of the entire fish stock and not merely the commercially caught component of the fishery. However, it is surprisingly hard to get representative samples of population size structure because of gear selectivity (size classes, sexes, and species may be differentially selected by the fishing gear), spatial changes in distribution with increasing size, and the difficulty in obtaining random samples from catches (Hilborn and Walters 1992; Pennington et al. 2002). As fisheries develop, fishermen may alter fishing gears, expand into deeper waters (containing larger fish), start fishing in different areas, or target different components of the population (spawning aggregations vs dispersed individuals) (Hilborn and Walters 1992). At a minimum, it seems prudent to analyze length- and age-frequency data separately for each gear type and area fished and to downweight age- and length-frequency data used in stock assessment models by assuming that effective sample sizes are much smaller than the actual number of fish measured (Pennington et al. 2002).

CPUE indices

The analysis of CPUE plays a disproportionately large role in fisheries stock assessments because CPUE data is relatively cheap and easy to collect compared with other stock assessment inputs. The simplest assumption in using CPUE data is that trends in CPUE are linearly related to abundance. Unfortunately, CPUE is the most likely of all data inputs to be influenced by fleet dynamics and fishermen behavior, including increases in fishing power, information sharing, switching between target species, and many other factors. Only a brief summary of this subject is included here, as it would be better treated in a separate paper.

Fishing power tends to increase over time for various reasons, depending on the fishery involved; thus it is naïve to expect restrictions on nominal effort to constrain actual fishing mortality. In the Finland herring fishery, for example, the number of fishing trawls remained constant, but improvement in net design resulted in their average size increasing by a factor of 2.7 over two decades (Fig. 1) (Rahikainen and Kuikka 2002). In the Australian northern prawn fishery, despite nominal effort reductions of 39%, adopting GPS (global positioning system) and plotter increased fishing power by 12% in 5 years through more accurate targeting and charting of fishable areas (Robins et al. 1998). Stock assessments should therefore take into account the disparity between nominal effort and true fishing power, while management

Fig. 1. Number of trawls of different sizes (*s*; m) employed in the Finland herring (*Clupea harengus*) fishery. Modified from Rahikainen and Kuikka (2002).



policies should attempt to constrain actual fishing mortality and not nominal fishing effort.

Information transfer allows fishermen to reduce the time they spend searching for aggregations. If the fish stock declines, but search time remains low, CPUE will hardly decline, breaking the assumption of proportionality between CPUE and abundance. Information transfer is widespread but varies greatly depending on the size of the fishing community, relatedness of participants, differences in ethnicity, and the biology of the species involved (sedentary or mobile). Active information transfer is when direct communication is used between fishermen, typically between close relatives and long-standing friends, such as that observed in the Maine lobster fishery (Palmer 1991) and the southeastern Alaskan salmon purse-seine fishery (Gatewood 1984*a*). Passive information transfer occurs when fishermen observe other fishermen and is most common when targeting highly migratory or mobile species; in such cases, a combination of exploration and following other vessels will increase catch rates (Mangel and Clark 1983; Vignaux 1996; Ruttan 2003).

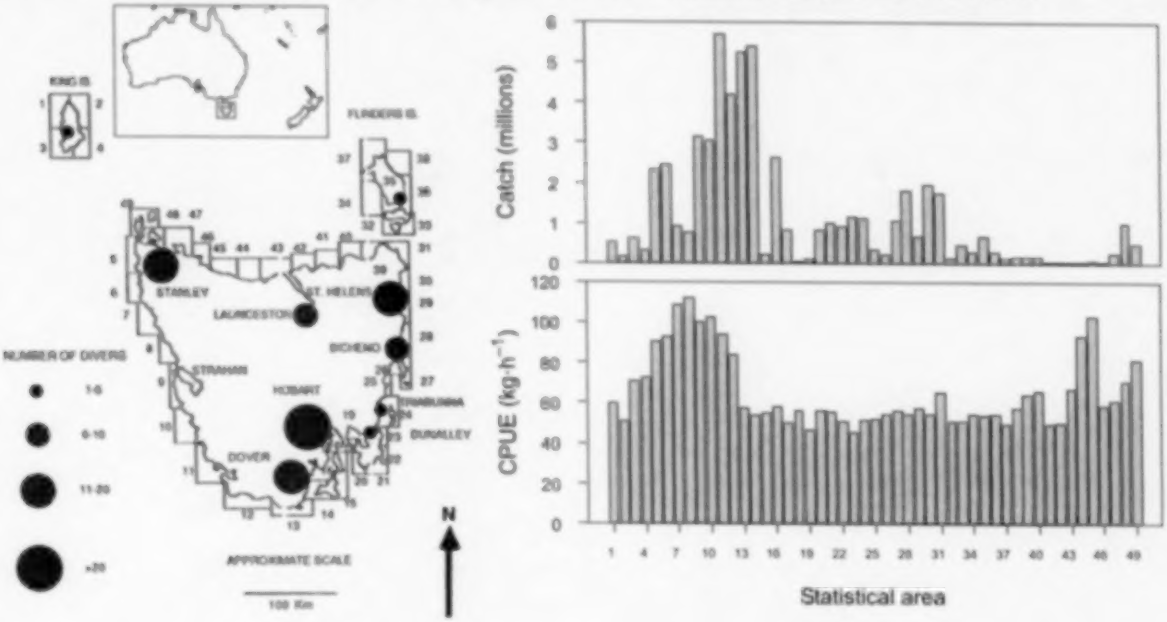
In multispecies fisheries, the target species may change from trip to trip or even from trawl to trawl, making it difficult to estimate CPUE for any individual species. In the Danish fishing fleet, for example, there are 25 vessel groups targeting 54 fisheries, and there was evidence for shifting between gears and areas, especially in secondary fisheries (Ulrich and Andersen 2004). Fishermen will target the most valuable species where possible, but fluctuations in market prices and allowable catches of particular species could result in the targeting of different size classes (e.g., Béné 1996) or different species (e.g., Holland and Sutinen 1999), complicating the analysis of CPUE.

It might be thought that spatial patterns in CPUE can be examined to determine where fish are present at highest abundances and hence where productivity is greatest, but CPUE turns out to be surprisingly constant over large spatial areas in fisheries ranging from oceanic longline fleets to crabbers to abalone divers (e.g., Prince and Hilborn 1998; Fonteneau and Richard 2003; Swain and Wade 2003). The theory of the ideal free distribution (IFD; Fretwell and Lucas 1970) explains this phenomenon. The IFD predicts that when foragers have perfect knowledge about resources in a number of different areas and there is no cost to choosing among areas, then the attempts of each forager to maximize their profitability will result in an equalization of profit rates in all areas. At this equilibrium, the number of foragers (fishermen or fishing effort) in each area will reflect the abundance better than the profit rate (CPUE). Fisheries research in this field has been reviewed by Gillis (2003). It turns out that although fishermen do not have perfect knowledge and the average fishery is not in equilibrium, these assumptions are sufficiently well approximated in fisheries for the IFD to hold. A classic example is the Tasmanian abalone (*Haliotis rubra*) fishery (Fig. 2) in which CPUE is equalized among accessible areas, despite catches differing by several orders of magnitude (Prince and Hilborn 1998). CPUE was greater only on the west coast of Tasmania (Fig. 2), reflecting that region's inaccessibility and worse weather, which combine to reduce the number of days on which fishing can occur (Prince and Hilborn 1998). Thus, deviations from IFD predictions generally point to violations of the underlying assumptions of free movement and perfect information, due to fuel costs, difficult terrain, poor weather, and other factors (Hilborn and Kennedy 1992; Prince and Hilborn 1998; Swain and Wade 2003).

There are thus many factors related to aspects of fleet dynamics and fishermen behavior that can reduce the comparability of CPUE among years and areas and obscure the relationship between CPUE and biomass levels. To detect CPUE signals, it has become common practice to standardize CPUE data to remove trends in vessel characteristics, fishing season, fishing ground, and other factors unrelated to stock abundance (Maunder and Punt 2004). However, even when CPUE series were standardized, a meta-analysis examining CPUE paired with independent research abundance estimates showed that in most cases (70%) there was evidence of hyperstability (when CPUE remains high while stock abundance declines) (Harley et al. 2001). An extreme example of this phenomenon occurred in the northern cod (*Gadus morhua*) fishery in which CPUE actually increased as the stock declined, leading to misleading stock assessments, unsustainable fishing mortality, and the eventual collapse of the stock (Rose and Kulka 1999). Hyperdepletion (when CPUE declines faster than abundance) is also a possibility when intense localized depletion of dense aggregations depreciates catch rates but does not greatly affect overall abundance (e.g., Sosa-Lopez and Manzo-Monroy 2002; Fonteneau and Richard 2003). Accordingly, the claims by Myers and Worm (2003) that the biomass (they actually examined CPUE) of oceanic predators was reduced by 80% within 15 years of industrialized fishing have recently been questioned (Polacheck 2006) because these rapid CPUE declines occurred during a period of historically low effort and catches, suggesting hyperdepletion.

In conclusion, either hyperstability or hyperdepletion should be suspected in every fishery because of the interaction between fleet dynamics and the spatial distribution of the resource. At a minimum, fisheries managers and scientists need to standardize CPUE data, to split CPUE series

Fig. 2. Catch (millions of abalone) and catch-per-unit-effort (CPUE; kg·h^{-1}) in the statistical areas of the Tasmanian abalone (*Haliotis rubra*) fishery (statistical areas shown in lower map; location of Tasmania off the southern coast of Australia shown in upper inset). Catches are summed over 1965–1986, CPUE is averaged over the same period. Modified with permission from Prince and Hilborn (1998).



when technology or fleet behavior changes, and to treat the resulting series with a healthy dose of skepticism.

Input controls

Stock assessments provide recommendations on what level of removal is appropriate for fish stocks, but fisheries managers must choose how to control catches. Management often starts with input controls, including restrictions on season length, engine horsepower, tonnage, hull construction, gear types, the number of crew members on board, and vessel entry. However, input controls almost always result in a less efficient fishery (both technically and economically) because they restrict methods of catching, instead of restricting catch directly. Changes in fleet dynamics can result in annual changes in the relationship between input controls and resulting catches, which can result in unpredictable annual catches, leading to overharvesting, and variation in fisheries employment levels. Furthermore, it must be borne in mind that under input controls, fishermen will try to maximize their share of the catch in a race for fish, leading to excessive investment in fishing technology.

Restrictions on season length

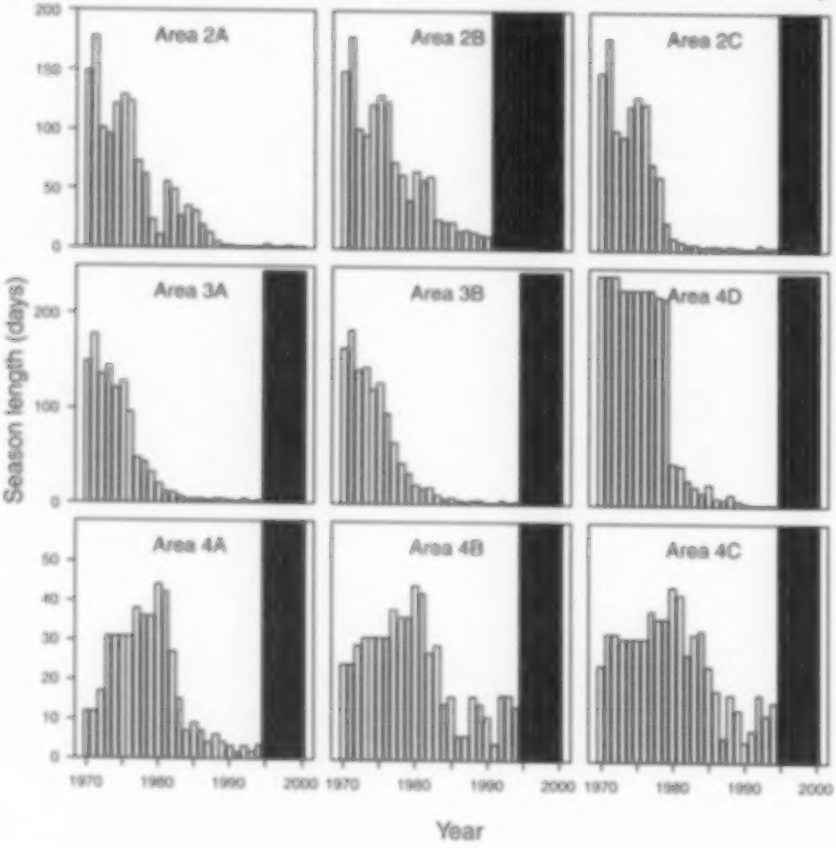
Closed seasons may be imposed to protect spawning periods and to limit catches. Experience shows that season-length restrictions are insufficient to control total fishing effort, especially in profitable fisheries. The incentives that were present under open access remain: new fishermen will continue to enter the fishery and existing fishermen will continue to increase their fishing efficiency and capacity, requiring further season-length restrictions. This pattern has been widely repeated in many fisheries, including those for Alaskan halibut (*Hippoglossus stenolepis*), with season lengths in each area decreasing from 40–230 days to just 1–11 days (Fig. 3), and for Alaskan sablefish (*Anopoploma fimbria*), with season length declining from 254 to 60 days in the Central Gulf and from 180 to 20 days in the Eastern Gulf (Pautzke and Oliver 1997).

Shortened fishing seasons have many negative effects. They disrupt the natural evolution from generalists towards specialists by preventing year-round fishing. They cause market gluts during season openings, which reduce the prices paid to fishermen and decrease the availability of fresh product to consumers (Pautzke and Oliver 1997). During the short, intense seasons, fishermen have to operate regardless of weather conditions, which may put boats and crew at risk. Fishermen may engage in capital stuffing (excessive investment in capital equipment) to maximize catch rates, dissipating profits. Finally, during the race for fish, excessive amounts of gear may be set but not retrieved or lost in the rush. Lost gear is a financial burden and also contributes to stock declines through "ghost fishing", because fish continue to be caught and killed by abandoned gear. The International Pacific Halibut Commission (IPHC 2000) estimated that almost 900 t of Pacific halibut, worth US$3.2 million, were killed in 1990 in abandoned gear (Hartley and Fina 2001). In summary, restrictions in season length may constrain total mortality, but the resulting intense race for fish leads to many negative outcomes.

Vessel and gear restrictions

Fisheries managers may attempt to reduce fishing effort by placing restrictions on vessel and gear characteristics. These restrictions directly reduce the economic efficiency of

Fig. 3. Changes in season length in nine management areas of the Pacific halibut (*Hippoglossus stenolepis*) fishery during 1970–2000: light bars, periods when fishing effort was controlled by season length; dark bars, management under individual transferable quotas (ITQs). Area 2A (Washington) is still managed by season length. The *y* axes differ for each horizontal row of graphs and the ITQ season lengths were 213–259 days in all cases. Sources: annual reports of the International Pacific Halibut Commission (e.g., IPHC 2000).



the fishing fleet, lowering profitability, and provide incentives for fishermen to invest capital in unregulated input dimensions (e.g., increasing vessel length when regulations restrict engine horsepower). When a fleet-wide TAC limits fishermen, they will overinvest in vessel improvements and in technology that may not be the most efficient for the fishery, resulting in suboptimal fishing practices (Wilen 1979).

One of the best examples of indirect regulations leading to economic inefficiency is the Bristol Bay sockeye salmon fishery (Metzner and Ward 2002). The fishery was originally valued at US$350 million but is now worth less than 10% of that because of a combination of overcapitalization and an increase in farmed salmon on the market (resulting in reduced prices). Initially, the number of vessels in the fleet was limited to reduce fishing pressure. Fishermen responded with vessels that were larger and faster than their predecessors. When restrictions were placed on vessel length, fishermen increased vessel width and engine power. The net result was that much of the potential profit in the fishery was lost to fuel costs and vessel improvements. In the late 1990s, more than 2000 high-powered boats caught the same amount of salmon as fewer than 1500 sailing vessels in the 1920s (Link et al. 2003).

Technical efficiency is a measure of how efficiently fishermen conduct harvest (the goal being to maximize the CPUE) and will be reduced by limiting vessel or gear characteristics. In Australia's northern prawn fishery, a vessel replacement program was started in 1985, with the limiting metric of each new vessel being a sum of engine power and hull size. In response, fishermen increased an unregulated input control (the length of the gear headrope), decreasing the average technical efficiency of the fleet (Kompas et al. 2004). Technical efficiency also decreased with vessel size in the Dutch beam trawl fishery when mesh size and beam length were restricted (Pascoe et al. 2001).

Gear restrictions may have unintended consequences. In the Alaskan red king crab (*Paralithodes camtschaticus*) fishery, the introduction of pot limits unexpectedly shifted wealth from large vessels to small vessels (Greenberg and Herrmann 1994). In the Maine lobster (*Homarus americanus*) fishery, pot numbers actually greatly increased after pot limits were imposed because good economic conditions favored entry, and part-time fishermen who formerly used small numbers of pots ended up increasing their pot numbers to the maximum allowed because they were concerned about the potential for future freezes in pot numbers (Acheson 2001). Finally, gear restrictions are vulnerable to the creativity of fishermen. For instance, when trawl nets were banned in the Florida finfish fishery, fishermen responded by fishing with tarpaulins instead of nets (Metzner and Ward 2002).

If vessel or gear restrictions are to be considered for controlling fishery effort, they must be enforceable and leave no unregulated inputs. The economic, biological, and social consequences must be considered, in addition to the inefficiency resulting from each restriction. Such considerations may limit the degree of overcapitalization and rent dissipation.

Limited-entry programs

Limited entry may be intended to prevent further increases in effort, to increase economic efficiency, or to protect local fishermen from outside competition and risk. However, limited entry rarely ends up reducing or limiting fishing effort. In the New Jersey (US) blue crab (*Callinectes sapidus*) fishery, for instance, a limited-entry program in 1993 did not restrict the number of pots allowed per boat, and by 1995, the total number of pots deployed in the fishery had actually increased by 8% (Stehlik et al. 1998). Studies of diverse types of fisheries catching lobster, salmon, and halibut have also demonstrated increases in fishing effort following the introduction of limited-entry regulations, even when limited entry is combined with vessel or gear restrictions (e.g., Fraser 1979; Meany 1979; Trumble et al. 1993; Townsend and Pooley 1995).

One problem with limited-entry programs is capital stuffing. When the total catch of the fleet is limited, each individual stands to increase their share of the catch by fishing harder, for example, by increasing the size of their vessels or by upgrading their engines when they replace their vessels. Although the 1969 limited-entry program in the British Columbia salmon (*Oncorhynchus* spp.) fishery decreased the number of vessels in the fleet (appearing to decrease effort), Fraser (1979) showed that gill-netters and trollers (employing 1–2 crew) were being replaced by purse-seiners (employing 4–5 crew) and by vessels with multiple sets of gear. This switch required an investment of capital in vessel improvement, increasing fishing costs and causing overcapitalization in the fishery. The Bristol Bay limited-entry program in 1974 resulted in similar vessel modifications, particularly for vessels with owners who were not local to the Bristol Bay area (Koslow 1982).

It should not be thought that limited entry offers no hope. On the contrary, limited entry is a necessary step in constraining overall fishing power, especially in profitable fisheries. The problem is that limited entry is typically introduced only when there is already evidence of overcapitalization or overfishing. An exception is the Western Australian prawn fisheries, in which limited entry was introduced during the exploration phase and economic rents were still being generated 15 years later (Meany 1979). In that case, a few large companies owned the entire fleet, which may have limited vessel improvements to those that would improve fishery-wide profits.

Although some limited-entry programs have been designed to protect local fishermen from competition, transferability of permits may reduce the protection offered. In the Bristol Bay salmon fishery, 6% of the original limited-entry permits were transferred from local residents to nonlocal fishermen between 1975 and 1979 (Koslow 1982). These changes occurred because residents were poorer and less economically flexible than nonresidents and thus tended to sell permits during economic crises when prices were lowest. Consequently, 41% of outsiders said their income increased under limited entry compared with only 4% of residents.

A limited-entry program needs to be designed in combination with season length, area, vessel, and gear restrictions to have even a chance of being successful (Adasiak 1979). If only a single aspect of the fishery is regulated, fishermen will likely increase effort using unregulated dimensions of the fishery, which may result in unintended consequences. If limited entry is intended to protect local fishermen, managers should consider whether to issue permits to individuals or vessels and whether permits should be transferable (Adasiak 1979). Inactive permits may become problematic if vessel buybacks are proposed, but requiring permits to be fished may lead to fishing even when the fishery is not economically viable (Townsend and Pooley 1995).

Area-based management

Spatial controls have long been part of fisheries management and are exercised over a wide range of scales. Catch, effort, vessel and gear restrictions, exclusions, and temporary or permanent closures are commonly specified by area. Spatial management may be based on existing political boundaries, species distribution, or the distribution of fishing effort. It seems intuitive that successful spatial management regimes would account for the behavior of fishermen.

Area-based management actions will impact the spatial allocation of effort by fishermen, because fishing location choice is an important component of fishermen behavior (e.g., Branch et al. 2005). Spatial allocation of effort is often related to distance from home ports (Sampson 1992; Caddy and Carocci 1999) and to other costs associated with different fishing areas (Prince and Hilborn 1998). Species profitability, catch rates, quota limits, and the relative desirability of specific fishing locations are all factors that may drive changes in fishing location (e.g., Hilborn and Ledbetter 1979; Gorfine and Dixon 2001; Salas et al. 2004).

Spatial management will have a more pronounced impact on fishermen who are area specialists (fish only in one area) than on fishermen who are movement specialists and fish in multiple areas (Hilborn 1985; Hilborn and Ledbetter 1985). In the British Columbia salmon purse-seine fleet, area specialists performed well in one area and poorly in another, reflecting a lack of knowledge about other areas (Hilborn and Ledbetter 1985). In contrast, movement specialists tended to be highly successful at finding fish regardless of the location (Abrahams and Healey 1990). Hilborn (1985) notes that a proposal of area licensing in the British Columbia salmon purse-seine fishery was met with strong opposition by some parties: "many fishermen have devoted years to learning which weeks are best for which areas, and area licensing would deny them the opportunity to use that information to their advantage".

Area-based management is often used to spread out fishing effort or to rotate effort between open and closed areas. Even without explicit management, fishermen may distribute their effort in this manner. Among abalone divers in Australia, incentives to maintain high catch rates led to patterns of effort rotation on individual reefs that mitigate against high exploitation rates (Gorfine and Dixon 2001). Fishermen may develop their own mechanisms to spread fishing out, avoid repeated harvesting, and reduce conflict, as has happened informally in the Aleutian Islands golden king crab (*Lithodes aequispinus*) fishery (Criddle et al. 2001) and formally in the stake-net fishery in Itoman, Japan (Akimichi 1984). Such examples demonstrate a tier of self-governance beyond that controlled by management regulations.

Reactions of fishermen to spatial management measures may be predicted through analysis of real data (e.g., Salas et al. 2004) or through fisheries models (e.g., Little et al. 2004). For example, Marchal et al. (2002) assessed the impact of the "plaice box", an area of restricted fishing in the North Sea. Although the fishing efficiency of some vessel classes increased inside this area, others did not, perhaps because of many other area-dependent factors besides the management action.

Marine protected areas (MPAs), or marine reserves, have been in use for over a millennium (Johannes 1978) and are a special case of area-based management. There has been growing momentum to set aside 20%–30% of the world's oceans to protect against human activities, including fishing, at an estimated cost of US$5–19 billion (Balmford et al. 2004). Proponents argue that closed areas will protect some portion of a stock from fishing pressure, increasing individual sizes and their contribution to spawning biomass, and that catch rates will increase outside MPAs through migration and larval dispersal. However, commercial fishermen are often opposed to marine reserves, fearing that any improvement in harvest levels outside reserves will be insufficient to offset the loss of former fishing grounds included in the reserves. The results depend largely on what happens to the displaced fishing vessels: do they exit the fishery (in which case they are worse off) or intensify fishing pressure outside the reserve (depleting fish stocks outside the reserves)? The IFD predicts that effort should move to places of highest catch rates, i.e., near the reserve perimeters where spillover effects are greatest, termed "fishing the line". Relatively little empirical evidence for this effect has yet been published. In the California Big Creek reserve, no evidence was found of fishing the line (Wilcox and Pomeroy 2003), but area closures off the northeastern US resulted in high levels of effort within 5 km of the MPA boundary, which corresponded to a doubling of revenue per hour within 4 km of the reserve boundaries (Murawski et al. 2005). Nevertheless, fishing the line could be important: Palumbi (2004) notes that fish spillover (a major reason for implementing MPAs) has only been well documented a few times and may be dependent on the intensity of fishing immediately outside the reserve.

When considering MPAs and other forms of area-based management, managers should therefore consider enacting short-term reductions in overall fishing effort to avoid the potential for depletion of fish stocks outside MPAs caused by displaced effort (Hilborn et al. 2004*b*). In addition, some compensation may be necessary to win support from fishermen who specialized in fishing areas that would be closed under any regulations.

Dedicated access privileges

There are many benefits to ending the race for fish that exists in open-access fisheries and changing the incentives in input-controlled fisheries that lead to capital stuffing and inefficient fishing. One solution is output controls through "dedicated access privileges" (US Commission on Ocean Policy 2004), in which a share of the TAC is allocated to specified participants or groups of participants and they can then choose when to catch their share. Dedicated access privileges include territorial rights, cooperatives, community development quotas, and individual transferable quotas.

Territorial rights

Systems of territorial rights include informal fishing territories, customary marine tenure, and territorial use rights in fisheries (TURFs). In all these cases, groups of fishermen have formal or informal rights to harvest fish in a particular area and to exclude other fishermen.

Informal fishing territories typically arise where it is possible to defend territories. In the Maine lobster fishery, groups of fishermen called "harbor gangs" have exclusive fishing rights near their harbors or around the islands from which they operate (Acheson 1975). Territories are defended initially by verbal threats but this may escalate into trap cutting if these warnings are ignored. In territories that were more rigorously defended, lobsters were larger, a greater percentage reached maturity, and profits were greater than in areas where territories were less well defined (Acheson 1975). More formal territorial arrangements have arisen in the Japanese Itoman stake-net fishery, in which more than 200 fishing locations are shared among fishermen according to a series of complex rules (Akimichi 1984).

Customary marine tenure systems are undergoing a resurgence in Oceania (Johannes 2002), despite premature reports of their demise (Johannes 1978). Many countries in Oceania have allowed customary village regulations to be accorded legal authority. As a result, villages have declared marine reserves, excluded outsiders from fishing in their waters, banned or restricted certain types of gears, and banned fishing on certain species. A number of success stories have arisen; for example, in Vanuatu, many villages have chosen to cease fishing for trochus for several years between harvests to maximize their income (Johannes 2002), a solution that would not be possible without tenure rights to the resource. Marine tenure systems bear similarities to Japanese-style cooperatives and are more likely to be enforced and supported by fishermen than top-down regulations imposed by central governments.

TURFs are a formal mechanism of assigning exclusive use rights over a particular fishery area to an individual or group (Christy 1982) and have been used in a diverse range of fisheries (e.g., Criddle et al. 2001). Their best-known application is in Chile, where a network of TURFs has been implemented to manage the gastropod loco with great success (Bernal et al. 1999). When TURFs were established, the former race to exploit locos over a very short season was replaced by a yearlong fishing season, resulting in a higher quality product fetching greater and more stable prices. TURFs allow for the rational exploitation of resources and, through ownership, provide incentives to maintain a sustainable fishery and to prevent poaching.

These types of territorial rights provide the long-term incentives for the resource owners to sustainably manage their resources and will work best if the owners have the ability to prevent outsiders from harvesting their resources.

Cooperatives

Fishery cooperatives are groups of individuals, each of which are allocated a share of the TAC. Individual allocation decisions are made within each cooperative, usually by agreement. Each cooperative is able to choose when and how to harvest their share of the TAC, halting the race for fish and preventing overcapitalization. In addition, the cooperative's knowledge of fish distribution, processing, and marketing can be used efficiently to improve profitability. Furthermore, cooperatives are effective at devising and enforcing self-imposed regulations that will be supported by local social norms (Townsend 1995). Cooperatives have been successfully employed in Japanese fisheries and in the US Pacific whiting (*Merluccius productus*), Bering Sea and Aleutian Islands (BSAI) pollock (*Theragra chalcogramma*), and Chignik Lake salmon fisheries (Kitts and Edwards 2003).

Since 1948, all Japanese fishermen must belong to cooperatives that allocate licenses and manage resources in specific coastal zones and often provide support services such as loans (Yamamoto 1995). Their overall success must be balanced against the possibility that allowable catches may not be sustainable and the lack of protection for migratory stocks that visit multiple zones (Yamamoto 1995).

In the BSAI pollock fishery, each company decides how many boats are necessary to catch their portion of the TAC. This has resulted in a 30% reduction in fleet size and a longer and more relaxed fishing season (North Pacific Fishery Management Council 2002). Instead of attempting to maximize catches, fishermen now target particular schools more accurately, deliver a higher quality product, and have increased product recovery rates for catcher–processor vessels by 35%.

In the Lake Chignik sockeye salmon (*Oncorhynchus nerka*) fishery in Alaska, 77 of the original 100 vessels formed a cooperative, agreeing to share their profits, and were allowed to catch 77% of the TAC in 2002. Only 22 of the 77 vessels were used to catch the same quantity of salmon, greatly increasing profitability and resulting in changed harvesting practices allowing for the transport of live salmon directly to the processors, ensuring higher fish quality for consumers. Lake Chignik salmon are now marketed as a special brand, Castle Cape Reds, and command premium prices (Babcock and Weninger 2004). Furthermore, the more relaxed and efficient fishing process has also allowed the fisheries manager to fine-tune the escapement levels in a much more responsive manner than before (G.S. Gislason & Associates Ltd. 2004).

Cooperatives avoid the problems of the race for fish while encouraging fishermen to abide by the regulations through common ownership and self-management. They are most applicable to fisheries with a limited number of participants, creating circumstances where social pressure can ensure sustainable fishing practices.

Community development quotas (CDQs)

When dedicated access privileges are granted to communities, these are termed community development quotas (CDQs). CDQs embody the concept that fishing communities have interests in fishing that go beyond just the harvesters and processors involved in the fishery (Ginter 1995). In the BSAI pollock fishery, 55 remote villages were initially allocated a total of 7.5% of the TAC as CDQs (Ginter 1995). Most villages rented out their CDQs to commercial companies to obtain additional revenue or required the employment of local labor in the fishery in exchange for their catch shares. The CDQ program provided many benefits to the remote villages, basically through the transfer of fishing wealth to meet social objectives.

Individual transferable quotas

Individual transferable quotas are a form of dedicated access privilege allowing maximum flexibility. Each ITQ holder is allowed to harvest a portion of the TAC in a given year and can transfer this right (or privilege) to other entities by leasing or selling it (Christy 1973). ITQ systems have been introduced in many countries and are the default choice of management in Iceland (Arnason 1996) and New Zealand (Sissenwine and Mace 1992; Annala 1996). Although it is deceptively simple to describe ITQs, their consequences are far-reaching and have been detailed in a series of reviews (e.g., Squires et al. 1995; Grafton 1996; National Research Council (NRC) 1999).

The key difference between ITQs and other forms of dedicated access privileges is transferability, which encourages less efficient owners to sell their quota to more efficient owners and leave the fishery, reducing overcapacity (e.g., Crowley and Palsson 1992; Wertheimer and Swanson 2000). Through payment for their quota, exiting vessel owners are compensated without requiring the public funds typically used in vessel buyback programs.

Under ITQs, fishermen have the most flexibility in choosing when and where to fish. A classic example is that of the Alaskan halibut fishery (Wertheimer and Swanson 2000; Hartley and Fina 2001). In this fishery, management by season-length restrictions resulted in capital stuffing, ever-shortening fishing seasons, gluts of halibut on the market, unsafe fishing conditions, and overcapitalization as fishermen competed against each other for the highest possible share of the TAC (Fig. 4). After ITQs were introduced, season length increased by one or two orders of magnitude (Fig. 3), the number of search and rescue missions decreased by 66%, the number of active vessels declined by 40% in the first year, and most of the halibut could be marketed fresh instead of frozen. In addition, catches were consistently kept under the TACs, and "ghost fishing" was reduced by 75% (Fig. 4).

The Icelandic summer spawning herring (*Clupea harengus*) fishery offers an example of the kinds of changes to be expected under ITQs (Fig. 5). Since this fishery reopened in 1975, total spawning biomass and landings have increased dramatically (although this is not directly due to ITQs). The

Fig. 4. The effects of individual transferable quota (ITQ) implementation (dark bars) on overharvest percentages, number of vessels, and estimated tonnage of fish caught by lost or abandoned gear (ghost fishing) in the Alaska halibut (*Hippoglossus stenolepis*) fishery, and search and rescue missions in the Alaska halibut and sablefish (*Anopoploma fimbria*) fisheries. Sources: National Research Council (1999), Hartley and Fina (2001), Wertheimer and Swanson (2000).

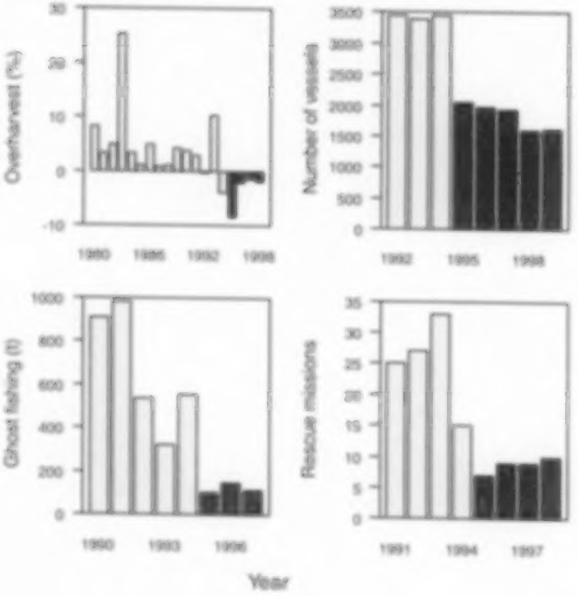
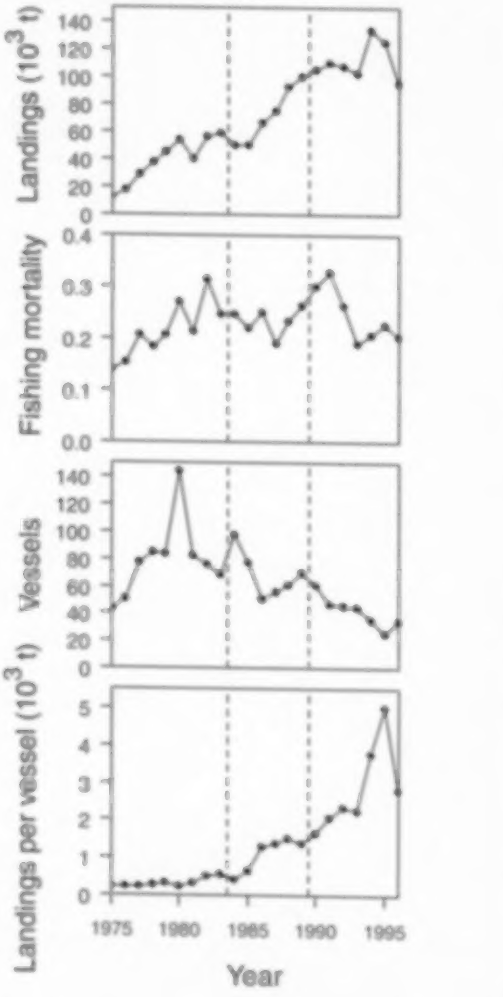


Fig. 5. Landings (10^3 t), fishing mortality, number of purse-seine vessels, and landings per purse-seine vessel (10^3 t) in the Icelandic summer-spawning herring fishery (*Clupea harengus*) during 1975–1996. Entry was not restricted before 1982. In 1982–1983, a lottery was used to halve the fleet size. Periods with no individual quotas, limited transferability of individual quotas (1984), and full transferability (i.e., ITQs, 1990) are divided by broken lines. Modified from Jakobsson and Stefánsson (1999).



number of vessels initially increased threefold, but when individual quotas were introduced, this increase reversed. The decline in vessel numbers accelerated when fully transferable ITQs were introduced in 1990, despite further increases in landings. In an open-access fishery, the opposite pattern in vessel numbers would be expected. As a result, landings per vessel increased by an order of magnitude (Jakobsson and Stefánsson 1999).

Under ITQs, biological sustainability is controlled by the TAC, while economic success is not only allowed, it is encouraged. Fishermen change their behavior in a variety of positive ways to maximize their profits. They typically aim for higher prices by increasing the quality of their product, changing the product form from frozen to fresh, adding value to the product, fishing when market prices are high (which may increase fishing in dangerous conditions), or changing fishing patterns to obtain a broader mix of species (Casey et al. 1995; Batstone and Sharp 1999).

The increased security granted by ITQs may also lead to unexpected behavior. ITQ shares become a valuable asset that approximates the long-term value of the fishery, and fishermen try to maximize this asset value. In the Gisborne rock lobster (*Jasus edwardsii*) fishery in New Zealand, ITQs were implemented in 1990 but catch rates continued to fall, partly due to the robbing of lobster traps by nonquota holders, but also because of octopus mortality on sublegal-sized lobsters held in the traps (Breen and Kendrick 1997). After 3 years of ITQs, the quota holders proposed halving the TAC to rebuild the stock, moving to a winter season when poor weather would reduce trap robbing and reducing the legal size to decrease octopus mortality (because allowing the retention of a greater proportion of legal-sized lobsters decreased the number of trap hauls needed to catch the TAC). The resultant changes have been remarkable: catch rates increased fivefold, the size and numbers of lobsters increased, illegal poaching diminished, and the value of ITQ shares increased sixfold.

ITQs may provide the correct incentives for fishermen to maximize profits without overfishing, but they also provide incentives to cheat. Fishermen can increase profits if they exceed their quotas, either through illegal fishing or by misreporting catches (Copes 1986). In addition, ITQs may provide incentives to increase high-grading and discarding (defined below), especially in multispecies fisheries where constraints on TACs for some species would restrict catches of other species and there is no individual accountability for discards (Copes 1986; Arnason 1994; Annala 1996). Fishermen may speculatively enter new fisheries, anticipating that a history of high catches may result in them being granted a large ITQ share in the future, and once an ITQ fishery is declared, vessels exiting the fishery may create a spillover effect of excess capacity into unrestrained fisheries (NRC 1999; Macinko and Bromley 2002).

Many social changes occur under ITQs. Quota owners generally have increased bargaining power compared with crew members, processors, and fishing communities, which may lead to fewer (but often better paid) crew members (Crowley and Palsson 1992; Wertheimer and Swanson 2000), processors being worse off than under a race for fish (Matulich et al. 1996; Matulich and Clark 2003), and fishing communities losing their quota (Eythórsson 2000). ITQs may also lead to increased concentration of quotas in the hands of a few people or large companies (Eythórsson 2000; Stewart and Callagher 2003). A combination of these issues has led to widespread dissatisfaction with the ITQ system in Iceland, including strikes by crew members protesting the low wages offered by quota holders under ITQs (Eythórsson 2000). These social changes are an inevitable consequence of the greater economic performance achieved under ITQs.

Thus, although ITQs offer many benefits to fisheries managers, modifications may be required to reduce some of their social impacts. A sensible list of recommendations is made by the NRC (1999) and includes improved monitoring and enforcement, restrictions on quota transfer and leasing, including crew members and fishing communities in initial allocations (e.g., through CDQs), and setting control dates for catch history well in advance to discourage speculative fishing. These modifications generally restrict the transferability or ownership rights conferred under ITQs, providing a tradeoff between economic efficiency and societal goals.

Advantages and disadvantages of dedicated access privilege systems

All dedicated access privilege systems allow fishermen greater flexibility in deciding how to fish compared with alternative management structures. These systems therefore promote economic efficiency, improve profitability, reduce overcapitalization, and result in a better quality of product. By restricting access and fishing privileges to particular groups, they provide incentives for resource stewardship. However, the process of granting fishing privileges is often contentious, and this can cause social impacts related to the creation of a class of people that have control over fisheries access. Nevertheless, if such systems are designed carefully, they provide appropriate incentives for fishermen to balance resource stewardship, economic efficiency, and social welfare.

Bycatch, discards, and high-grading

Bycatch, discarding, and high-grading may affect the management of fisheries in a variety of ways. We define "bycatch" as the unintended catch of nontarget species, "discarding" as caught individuals that are returned to the sea, and "high-grading" as the practice of discarding less valuable grades of fish in order to fill quotas with more valuable grades. Discarding occurs in most fisheries (and may even be required) because fishing is imperfect: some caught individuals are too small, others are the wrong species, and still others may be diseased or damaged.

Estimates of worldwide discards of fish have decreased substantially from the widely quoted 27 million t per year in the late 1980s and early 1990s (Alverson et al. 1994) to current estimates of 7.3 million t in 1992–2001 (Kelleher 2005). The prime culprits are trawl fisheries, particularly for shrimp but also for demersal finfish (Kelleher 2005). In shrimp fisheries, discards are generally small fish with little value that would be more profitably harvested when larger (Hall et al. 2000).

High-grading occurs in fisheries that have individual output controls, such as bag limits, trip limits, and individual quota systems, in which there is also a price differential between different sizes of fish and little effort is needed to catch fish to replace those discarded (e.g., Arnason 1994; Gillis et al. 1995). High-grading was regarded as a problem in the New Zealand snapper (*Pagrus auratus*) fishery (managed by ITQs) in which some fish met the strict criteria for the lucrative *ike jime* Japanese market and could be sold for US$3 per kg more than those destined for the domestic market (Boyd and Dewees 1992). Increased enforcement and severe penalties reduced the level of high-grading in this fishery, and fishermen reacted by altering their handling and fishing practices to increase the proportion of *ike jime* fish; however, problems with misreporting and black market sales of the lower-value fish remain.

In multispecies fisheries managed with individual output controls, discarding problems may be exacerbated as fishermen have incentives to discard when quotas are exceeded so that they can continue fishing for another species (Copes 1986; Pikitch et al. 1988). One solution is seen in the multispecies British Columbia groundfish fishery in which there is 100% observer coverage and deduction of discard mortality from individual quotas and vessels are prohibited from bottom trawling for the remainder of the year if their individual quotas are not covered by leasing quota (Turris 2000). This system has led to near-zero discards of marketable fish (Branch et al. 2006).

Bycatch can be reduced using bycatch reduction devices (BRDs), gear modifications that attempt to exclude bycatch species from the target species' gear (Hall et al. 2000). BRDs can be beneficial to fishermen: in Australia's northern prawn (*Penaeus* spp.) fishery, studies showed that fishermen installing BRDs would increase their profits, as a result of a reduction in prawn damage from large bycaught animals (worth US$1 million fleet-wide), reduced time required to sort out small fish, and an easing of pressure from conservation groups (e.g., Salini et al. 2000). BRDs were subsequently made mandatory in the northern prawn fishery (Salini et al. 2000). In this and other prawn fisheries of Australia, the majority (100% in one fishery) of fishermen have adopted BRDs developed in conjunction with industry even before they were required by regulations (Kennelly 1999). Of course, if BRDs reduce catches of the target species and decrease fishing profitability, it is likely that fishermen will experiment with or modify these devices or resist their imposition

(Moberg and Dyer 1994). Thus the predicted reductions in bycatch may not in practice be realized.

Bycatch species may be charismatic and popular (e.g., dolphins and turtles). In the 1960s and 1970s, hundreds of thousands of dolphins were killed annually by purse-seine fleets fishing on tuna associated with dolphin schools in the Eastern Tropical Pacific. Public outcry and concern about declining dolphin populations led to the passage of the US Marine Mammal Protection Act in 1972. This Act capped the annual mortality of dolphins, placed observers on US vessels, and changed fishing gear and practices. Annual dolphin mortality declined from 500 000 to 20 000 in the late 1970s. However, the increased costs associated with these restrictions encouraged many US vessel owners to register their vessels with other countries that imposed fewer restrictions, and dolphin kills soared to 133 000 in 1986. However, a consumer boycott of dolphin-unfriendly tuna (starting in the late 1980s), the implementation of individual vessel quotas for dolphin bycatch (replacing fleet-wide limits), and 100% observer coverage on large vessels combined to reduce annual dolphin kills to 1877 in 1998 (Fig. 6), i.e., less than 0.1% of any dolphin population (Hall et al. 2000). The lesson from this case study is that although methods existed even in the 1970s that could reduce dolphin mortality, there were no economic incentives for fishermen to implement these methods. The key developments in this fishery were the creation of individual accountability of dolphin catches, increased market pressure from the dolphin-friendly tuna campaign, and 100% observer coverage on vessels.

Senescent fisheries

Fisheries that are heavily depleted require drastic management action, which may include fleet reductions, catch cuts, or even fishery closures. The costs of reducing fishing effort may be considerable and may include vessel buyback programs and the payment of unemployment insurance to ease the blow to fishermen and fishing communities.

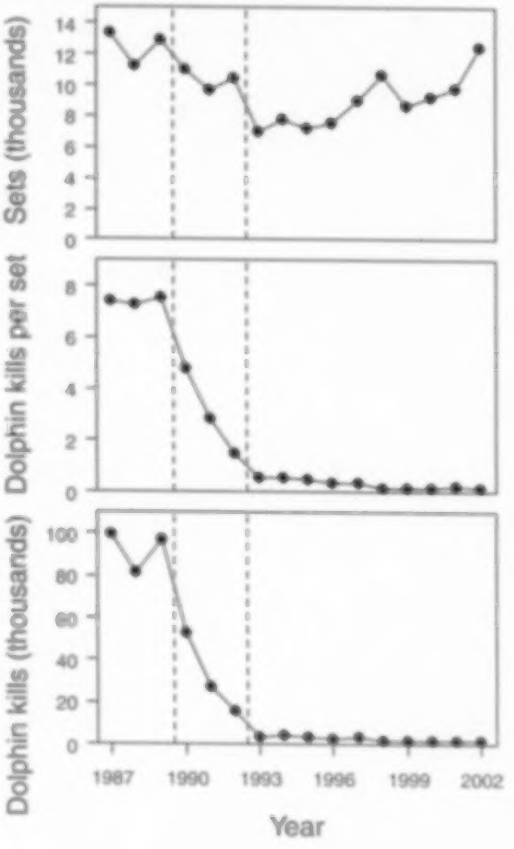
Vessel buybacks

Vessel buyback programs are widely used to reduce overcapitalization in depleted fisheries. The majority of academic attention has focused on how to remove the greatest fishing capacity for the lowest price. We examine the extent to which capacity is actually removed in buyback programs and the behavioral response of fishermen to these programs.

One common assumption is that removing vessels with the highest catch history for the lowest cost will be optimal (Holland et al. 1999), but the effectiveness of this approach may be undermined if vessel characteristics are not the most important determinant of catching power. If the vessel operator explains most of the variation in catch rates instead (the "skipper effect"), then any effect of removing vessels may be counterbalanced by these skilled individuals re-entering the fishery on other vessels.

Although the skipper effect is "widely recognized in the fisheries literature" (Squires and Kirkley 1999), Pálsson and Durrenberger (1982) found that among Icelandic cod fishermen, the size of boats and number of trips explained most of the variance in catch and that years of experience were not correlated with fishing success. Their thesis sparked intense debate (e.g., Gatewood 1984*b*; Pálsson and Durrenberger 1984). In response, Hilborn and Ledbetter (1985) found that "skipper, crew and net effects" accounted for 20%–24% of the variance in catch among British Columbia salmon fishermen, whereas vessel attributes including length, tonnage, and horsepower accounted for only 10%. Moreover, when localized skills specific to an individual fishing area were considered, the skipper effect accounted for almost half of the variation in catch. Pálsson and Durrenberger (1990) concluded the debate by contending that they began their research from the perspective of the Icelandic "folk model", which holds that skipper ability is responsible for nearly all of the variation in catch, and found less skipper effect than predicted by such a model, whereas Hilborn and Ledbetter (1985) "started with an opposite folk model — a model held by biologists who insisted that individual differences among skippers were unimportant — and showed that they were more important than the model suggested".

Fig. 6. Number of purse-seine sets, dolphin kills per set, and total dolphin kills in the Eastern Tropical Pacific purse-seine tuna fishery, 1987–2002. Major events indicated by broken lines include the 1990 decision by the three biggest tuna buyers to accept only dolphin-friendly tuna in response to a consumer boycott, and the 1993 La Jolla agreement that implemented vessel-specific dolphin catch limits. References: Gosliner (1999), Inter-American Tropical Tuna Commission (2003).



The obvious policy recommendation is to require buyback participants to leave a fishery altogether. Indeed, allowing vessel buyback participants to remain in a fishery may negate the effects of the buyback in unexpected ways as buyback participants may use the money that they receive to upgrade remaining vessels that they own. In the 1975 buyback in the Washington state salmon fishery, "nearly 40% of the participants in the program sold an unwanted license or vessel, upgraded vessels and gear, and remained in the industry" (Kurt and Muse (1984), personal communication, cited in Holland et al. 1999).

An additional problem of vessel buybacks is that they do not remove the incentives for the remaining fishermen to engage in capital stuffing, such as improved navigation aids, larger nets, more powerful winches, and greater fishing capacity (Clark and Munro 2002). Holland et al. (1999) raise an additional concern that even if fishermen and vessels depart from the fishery, "human capital" can still be passed on to the remaining fishermen in the form of logbooks, electronic records, and plotters that record the speed and location of vessels.

Buyback programs may also cause a "spillover effect" into other fisheries (Clark and Munro 2002). The vessels that are bought back are typically prohibited from future involvement in some sphere surrounding the fishery of interest, which may include that fishery, fishery management zone, state, or nation. However, buyback vessels may be sold or moved outside that sphere of influence. It is common knowledge that many Canadian "buyback seiners" have been purchased in the past decade by American fishermen for use in Alaska's decidedly overcapitalized salmon fisheries.

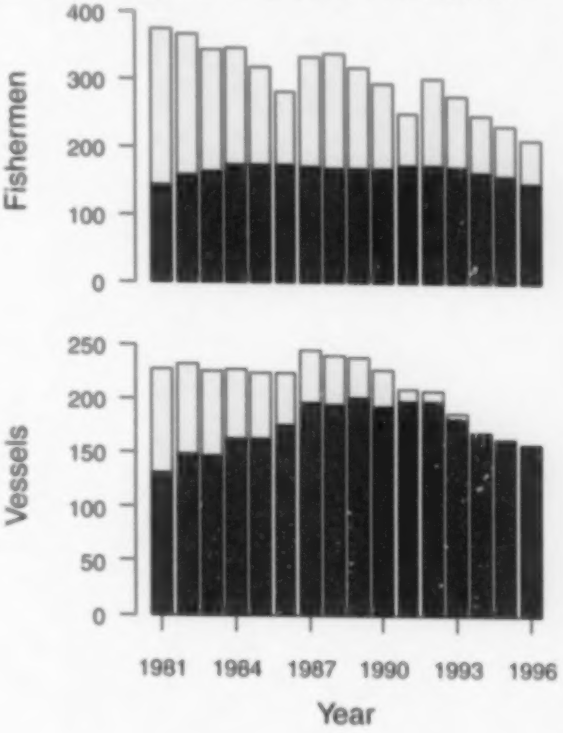
In summary, many buyback programs are not adequately structured to ensure the actual removal of fishing capacity along with the removal of vessels. Whatever capacity is removed may be compensated for by capital stuffing in the fishery or exported to cause overcapitalization in other fisheries. Additionally, buybacks increase the long-term incentives to build boats because they create an expectation that the reduction of excess capacity will be compensated in the future (Clark and Munro 2002).

Fishery closures and disaster relief

Moratoria and drastic catch reductions have been implemented repeatedly, along with a wide array of social programs, including subsidized loans, unemployment benefits, subsidized alternative employment, and "retraining" programs. With the exception of unemployment insurance, scant attention has been focused on the incentives created for fishermen by these measures.

Fishery participants have met proposed fishery closures and severe reductions in catches with responses ranging from intense opposition to cooperation. In the case of the New England groundfish fishery, participants have consistently opposed plans aimed at rebuilding the stocks, despite expected long-term increases in fishery output (Hilborn et al. 2004*a*). The authors pointed out that only a fraction of the fishing licenses were active, and hence a rebuilt stock would cause the activation of more licenses, canceling any benefits from stock rebuilding gained by the current participants. On the other hand, Irish-moss harvesters in the southern Gulf of St. Lawrence became keenly interested in conservation when depletion of the stock became evident (Pringle 1985). They voted against allowing the use of a piece of equipment designed to increase efficiency on the grounds that it might enable the clandestine use of a similar, ecologically destructive device. The main goal in this fishery was not to increase efficiency and profitability, but to ensure that as many fishermen as possible could continue working in the fishery for part of the year, thus qualifying for unemployment insurance during much of the remainder of the year.

Fig. 7. Numbers of registered full-time (dark bars) and part-time (light bars) fishermen and vessels registered to full-time and part-time fishermen in nine fishing communities in northeastern Newfoundland, Canada. The northern cod (*Gadus morhua*) moratorium was imposed in July 1992. Modified from Woodrow (1998).



After the collapse of the Canadian northern cod fishery (and despite a moratorium), only 10% of full-time fishermen surrendered their groundfish licenses in a buyback program, far short of the expected 50% (Woodrow 1998). One of the important reasons for retaining a license was that income support from relief packages depended on owning a license, and a minimum of 12 weeks of annual employment was required to qualify for unemployment insurance. Instead, fishermen increased effort on other species, such as crab and flatfish, and only part-time fishermen left the fishery (Fig. 7). The remaining crew members each work the minimum amount of time necessary to qualify for unemployment insurance and then quit to make room for others to do the same (Schrank 2005). Similar practices exist in the processing sector so that "the union ensures these people get their 12 weeks" (Woodrow 1998).

In summary, the full effects of disaster relief programs have not been thoroughly analyzed, but unemployment insurance acts as a subsidy that keeps fishermen in a fishery regardless of its profitability.

Compliance and enforcement issues

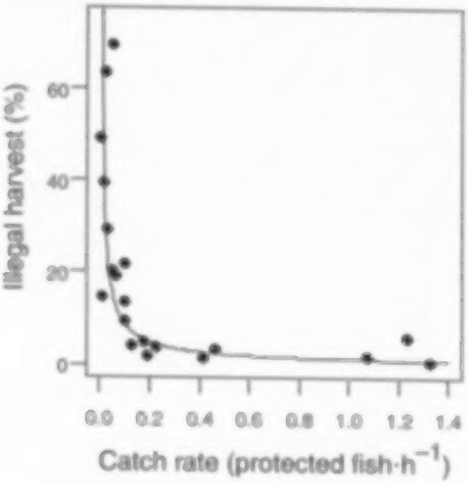
Given that fisheries management is about managing fishermen and not fish, the absence of an effective enforcement regime is likely to doom even the most robust fisheries management systems (Randall 2004). Therefore, management schemes that minimize the incentive for noncompliance and facilitate effective enforcement are ultimately the most successful at achieving fisheries management objectives.

The reasons for noncompliance are poorly understood and vary between different fisheries and the individual fishers themselves. Although economic incentives are undoubtedly important, fisheries managers need to also examine how normative and social factors influence fishermen behavior and response to enforcement. Incentives for illegal harvesting also vary with the status of the stocks, increasing when stocks are at low levels. In recreational fisheries, for example, Sullivan (2002) found illegal harvest increased sharply at low catch rates (Fig. 8), thereby placing further pressure on already depleted fish stocks. This has serious implications for fisheries managers attempting to protect declining fish populations, because just when effective protective regulations are needed most, the typical response of many fishermen is increased noncompliance.

Designing an enforcement system that elicits the desired behavior from fishermen requires intensive monitoring and high penalties for offenders, which are difficult and expensive to implement. For example, Namibia has expended considerable resources in enforcement of its exclusive economic zone, combining maritime surveillance, high levels of observer coverage, intensive port monitoring, and the seizure of numerous vessels (Bergh and Davies 2004). These measures greatly increase the risk of being caught fishing illegally in Namibian waters and make the expected costs of noncompliance so high that rational participants will choose to comply. Similarly, intensive measures employed in the British Columbia groundfish trawl fishery (Turris 2000) have also resulted in low levels of noncompliance (Ainsworth and Pitcher 2005).

The deterrent penalties in many fisheries are, however, inadequate to modify fishermen behavior (Blewitt et al. 1987). In such cases, crime pays, and many fishermen view monetary penalties simply as a cost of doing business (Frailey and Taylor 1987; Sutinen et al. 1990). Increasing the severity of penalties reduces the incentives to fish illegally but also results in more vigorous opposition to paying fines and fishermen taking "greater pains" to hide their illegal activity (Frailey and Taylor 1987). Fishermen can be highly creative in evading regulations: in the Atlantic sea scallop (*Placopectin magellanicus*) fishery, skippers have even built false bulkheads and storage compartments to hide illegal catches (NOAA 2004), in addition to the more mundane activities of skippers and processors conspiring to under-report catches and falsify records (NOAA 2005). In the absence of effective enforcement and compliance, routine violations may indicate that a norm of noncompliance has become established in a fishery (Sutinen et al. 1990).

Fig. 8. Relationship between catch rate and illegal harvest rate in 20 walleye (*Sander vitreus*) fisheries in northern Alberta, Canada. Fish are "protected" by minimum size limit or slot limit regulations. Modified from Sullivan (2002).



In short, despite management's best efforts, the determined violator can circumvent nearly any monitoring system employed to manage and enforce a fishery. Enforcement will be easier when it is in the interests of the fishermen to comply, either because the penalties are high or because of a long-term interest in the fishery. Simple regulations that are easy to enforce are most likely to avoid the development of a norm of noncompliance in a given fishery.

Summary

What has been learned

The central thesis of this review is that fisheries management is people management, and fisheries managers need to understand how individuals and fleets behave in response to regulation in order to design fisheries management systems that will achieve the desired social, economic, and biological objectives.

Individuals and fishing fleets act rationally to maximize their individual well-being. If we understand the economic and social circumstances of the fishery, we can usually explain and indeed predict the consequences of policies. The classic "perversities" of fisheries (overcapitalization, increasing investment in technology, shortening fishing seasons, and political pressure for higher catches) are in fact rational behaviors that should be expected and can be predicted in the types of fisheries management systems that predominate worldwide.

At the core of the fisheries problem, and the first challenge for understanding fishermen behavior, is the race for fish. The race for fish is a natural consequence of individuals making decisions to maximize their well-being and will be expected to occur in any system in which individuals can obtain a larger portion of the catch by fishing more or fishing more efficiently.

A wide range of techniques have been employed by management agencies to try to achieve economic and biological sustainability, with most fisheries in industrial countries going through periods of unregulated open access, TAC-managed open access, and TAC-managed limited entry. It is now recognized that the natural dynamics of fishing fleets during this sequence of regulatory systems lead to most fisheries being overcapitalized, heavily exploited, and neither economically nor biologically sustainable. Within all of these management systems, individuals can increase their catch by fishing more or more efficiently, and all lead to a race for fish. We have reviewed the range of alternative governance systems that are currently under consideration, or in use, to try to move from the "senescent" state of overcapitalized and overexploited to a more desirable state. The successful governance systems all have at their core a change in structure so that there is no race for fish.

The use of subsidies and buyback programs has generally not been successful, whereas various "dedicated access privileges" have been more successful. Subsidies and buybacks leave the race for fish intact, providing continued incentives for those remaining in fisheries to fish more or more efficiently. The more successful buyback programs have been associated with a move between a race-for-fish management and a dedicated access system, with the buyback being part of a total package that in the end eliminates the race for fish. Dedicated access systems include territorial fishing rights, cooperatives, community development quotas, and various forms of individual fishing quotas (e.g., ITQs). In each of these systems, allowable catches are allocated to individuals or groups to eliminate the incentives associated with the race for fish, and the participants naturally act in a fashion that maximizes their well-being, with generally desirable consequences. Problems have been identified with dedicated access systems, particularly for ITQ systems, which are the most common and best studied. Although ITQ systems do generally appear to achieve many of the economic objectives of fisheries management, concentration of ownership, negative impacts on processors, and other issues have been noted. Again, these outcomes are natural consequences of individuals acting rationally, and managers need to determine what the objectives of the system are and design the rules of the dedicated access system to provide incentives to achieve the management objectives.

Ecological and economic theories provide powerful tools to predict many aspects of fleet behavior. For example, the IFD generally explains the distribution of fishing effort across space and the consequent distribution of catch rates (e.g., Gillis et al. 1993). Given the importance of catch rates in the economics of vessel operation and the analysis of fisheries catch and effort data as indices of stock abundance, this theory has a particularly important place in the analysis of fishing fleet behavior.

Another recurring theme in the history of fisheries is the evolution of catching efficiency and the ability of fishing fleets to increase their fishing power despite attempts by management to prevent it. This is again a natural consequence of the incentives provided in systems with a race for fish and should always be expected. Although there are a number of statistical methods of "standardizing" catching power, the more challenging problem is determining the underlying relationship between catch rates and actual abundance.

Discarding, bycatch, and mortality of protected species is an area of growing concern, and the incentives provided in dedicated access systems that stop the race for fish do not generally provide appropriate incentives to reduce these actions. Successes in reducing these problems have involved additional incentives, such as bycatch quotas and prohibitions on discarding. These incentive systems almost always involve intense at-sea monitoring, which may indeed turn out to be essential for successful management of many fisheries.

Compliance and enforcement are often the neglected aspects of fisheries management, yet in many fisheries, illegal harvesting may be the major conservation issue. Our review suggests that the same forces are acting: individuals act rationally, and when the economic or social benefits of illegal activities exceed the costs (probability of detection and arrest combined with penalty size), illegal activities will be common. Successful fisheries management systems must find ways to reduce the benefits of illegal activities and increase the costs. Dedicated access systems have a good track record of making legal harvesting more profitable, increasing the potential deterrence (because access privileges can be revoked), and providing incentives for long-term stewardship of the resource. As such, dedicated access systems may be considered a good step towards better compliance. It is clear that good enforcement measures do significantly deter illegal activity and should be considered an integral part of any fishery management system.

The overall lesson that we have found in this review is that the behavior of fishing fleets and fishermen can be guided towards desirable actions by providing appropriate incentives. Responses of individuals and fishing fleets to management systems can be predicted based on individual utility maximization, and managers need to understand the economic and social forces affecting individual behavior when designing management systems. There are a range of governance structures that have provided appropriate incentives to stop the race for fish and reduce discarding and bycatch. Fisheries managers around the world need to learn from these lessons and move to systems with appropriate incentives.

What remains to be done

While much has been learned from the lessons of the past, there still remains much to be discovered. We are lacking models for the rational development of new fisheries. How do we balance incentives to develop and explore, while still capturing much of the economic value of these new fisheries for the public owners? Perhaps there are more lessons available than we have been able to ascertain in this review, and a review of lessons from developing fisheries should be initiated. What has emerged is that there is a need for biological caution in new fisheries, as these are low information resources. There are also strong arguments for the use of closed areas to protect a significant portion of the resource during fisheries development.

Another important area for research and exploration is the dynamics of group size and self-regulation in various dedicated access systems. Although we have examples of success in cooperatives, ITQs, TURFs, and CDQs, there is much to be learned about governance structures that work and those that do not. For instance, under what circumstances will these groups act as a single utility maximizing agent rather than collections of individuals? When will groups be effectively self-enforcing? How do we obtain the benefits of harvesting cooperatives without seriously disadvantaging existing processors?

The interaction between fisheries management systems and compliance and enforcement needs more study. There is a miniscule literature on this problem, perhaps reflecting the fact that branches or agencies separate from fisheries managers almost always conduct compliance and enforcement activities, and the compliance and enforcement agencies have traditions (for good reasons) of secrecy rather than publication of results and case histories. Studies that simply document the compliance systems and expenditures on compliance would be a good first step.

Perhaps the greatest problematic area is that of international and high-seas fisheries. These fisheries are often the last frontier of the unregulated fisheries of the past, inheritors of the "freedom of the seas" ethic. Designing international governance systems that provide appropriate incentives is an outstanding challenge. Where international governance is impossible, the power of public opinion and market pressure has in the past been successfully harnessed to prevent the overexploitation of depleted resources. There are many examples of nongovernmental organizations or campaigns that have had a major impact on international fisheries. The Greenpeace-initiated "Save the Whales" campaign played a major role in altering public opinion about whaling, which ultimately resulted in a moratorium on international whaling. The "dolphin-friendly" tuna movement resulted in a major change in tuna purse-seining operations and reduced dolphin deaths by several orders of magnitude. Finally, recent efforts by the Marine Stewardship Council to certify sustainable fisheries and by the Monterey Bay Aquarium (and others) to rate marine fisheries by sustainability may also have major impacts on the profitability of certain fisheries, perhaps forcing changes in fisheries exploitation even in international waters.

Fisheries managers are learning from experience, and in many countries, the lessons of the past have been absorbed and managers are moving to implement governance systems and incentives that eliminate the race for fish. However, the rate of learning is slow because of limited documentation of the lessons learned. Although this review will, we hope, be a substantial resource, a single review article is no substitute for a major body of case histories documenting the range of fisheries experience. We suggest that an international effort should be made to provide a broad range of case studies of fisheries management successes and failures that specifically explore the incentives of the management system and how individuals and fishing fleets have responded. Only by learning from the past will we do better in the future.

Fisheries management is people management, and the people involved in fisheries, be they harvesters, processors, scientists, or managers, act within a social and economic structure established by the governance systems. If we wish to achieve economically and biologically sustainable fisheries, we must recognize that people will act to maximize their individual well-being. Ludwig et al. (1993) argued that greed is the driving force behind fisheries overexploitation and collapse. Greed is really nothing more than an unrestricted desire to maximize individual well-being. We need to restrict and harness this "greed" to achieve socially desired outcomes. The lessons of the past suggest that appropriate incentives can do this and that individuals maximizing their well-being within an appropriate governance system should be an essential part of sustainable fisheries.

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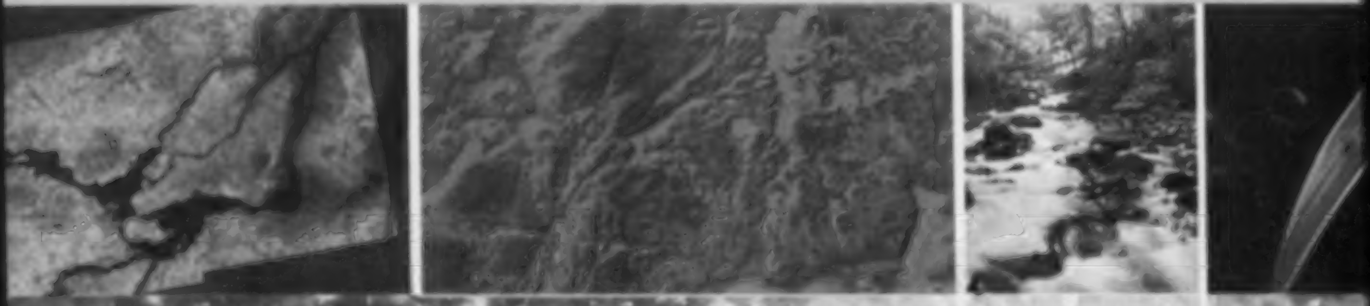

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